Liang *et al. Annals of Microbiology* (2024) 74:17
https://doi.org/10.1186/s13213-024-01762-x

Annals of Microbiology

UNIVERSITÀ DEGLI STUDI DI MILANO

REVIEW ARTICLE Open Access

Research progress on the polysaccharide extraction and antibacterial activity

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Abstract

Background Over time, the amount of germs resistant to antibacterial medications has been steadily rising because of their prolonged and indiscriminate use. The increase in drug resistance significantly threatens to human health and has become a globally recognized issue of concern. Therefore, identifying new antibacterial drugs is urgently needed.

Forward Polysaccharides are natural macromolecular substances that exist in plants, microorganisms, and animals, They have an immense amount of use in the food and medical industries. Polysaccharides can be categorized as plant, animal, or microbial based on the sources of the polysaccharides.

Conclusion Polysaccharides are natural compounds with antibacterial properties that exerts antibacterial activity by disrupting bacterial cell walls and cell membranes. They show potential as candidates for the creation and application of novel antibiotics. This article reviews the classification of polysaccharides, their isolation and purification, mechanisms of action, and antibacterial activity. The primary objective of this study is to lay down an empirical groundwork for examining the antibacterial properties of polysaccharides.

Keywords Antibacterial activity, Microorganism, Mechanism of action, Polysaccharide, Isolation, Purification

Introduction

Microorganisms are significant contributors to food spoilage, and certain pathogenic bacteria in food pose potential threats to human health and safety. Currently, the protracted and misuse of antibacterial drugs has resulted in an increase in bacterial resistance, with a notable increase in multidrug-resistant strains. However, the clinical efficacy of these antibacterial drugs is limited. To combat the emergence of multidrug-resistant strains, there is an immediate requirement for the research and implementation of innovative antibacterial medications.

Polysaccharides are natural polymers characterized by diverse chemical structures, typically comprising ten or more monosaccharides linked to sugar chains or branched structures. They are found predominantly in plants, animals, and microorganisms. The common plant polysaccharides include pectin, starch, and cellulose. The common animal polysaccharides include heparin, hyaluronic acid, and chondroitin sulfate. The common microbial polysaccharides include those from *Ganoderma lucidum*, xanthan gum, and *Lentinan*. A number of factors, such as the polysaccharides' molecular weight, functional groups, and extraction techniques, affect their antibacterial effectiveness. Natural polysaccharides undergo chemical modifications such as sulfation, phosphorylation, and selenium incorporation to optimize

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their biological activities. The bioactivity of polysaccharide has been widely researched in both the domestic and international scientific communities. It is essential since it not only in antitumor (Singdevsachan et al., 2016), antibacterial (Zhou et al. 2020), antioxidant (Pu et al. 2016), immunomodulation (Singdevsachan et al., 2016; Xie et al. 2016), regulation of intestinal flora (Xie et al. 2016), and anti-inflammatory (Li and Shah 2016) effects but also in reducing the teratogenicity, toxicity of synthetic chemicals, and potential carcinogenicity (Huang and Huang 2020).

Polysaccharides exhibit specific antibacterial activity against both gram-negative and gram-positive bacteria (Yu et al. 2019; Zhou et al. 2022; Meng et al. 2017). They are readily accessible, non-toxic, and have great potential for extensive use as novel antibacterial agents in medicine and food. The mechanisms underlying the antibacterial activity of polysaccharides are complex. Polysaccharides primarily exert antibacterial effects by compromising the integrity of the cell membrane and cell wall, inhibiting biofilm formation, influencing bacterial metabolism, disrupting protein synthesis, and impeding nutrient uptake. Antibiotics are frequently utilized as antibacterial agents, but the misuse of antibiotics not only results in the development of drug-resistant genes but also harms human health by disrupting the balance of intestinal microflora. In contrast, polysaccharides are considered safe, effective, and non-toxic to intestinal microflora (Sun et al. 2021).

Based on previous research, polysaccharides, as natural macromolecular substances, possess intricate structures, and their biological activities remain incompletely understood. Polysaccharides and their derivatives exhibit diverse applications as antibacterial agents and materials. To elucidate further the antibacterial potential of polysaccharides and to develop novel antibacterial agents, this article focuses on the categorization, isolation, and purification of polysaccharides, their antibacterial mechanisms, elements impacting antibacterial efficacy and the use of polysaccharides in antibacterial medications, see Fig. 1. This study offers a conceptual basis for the subsequent exploration of polysaccharides with antibacterial properties.

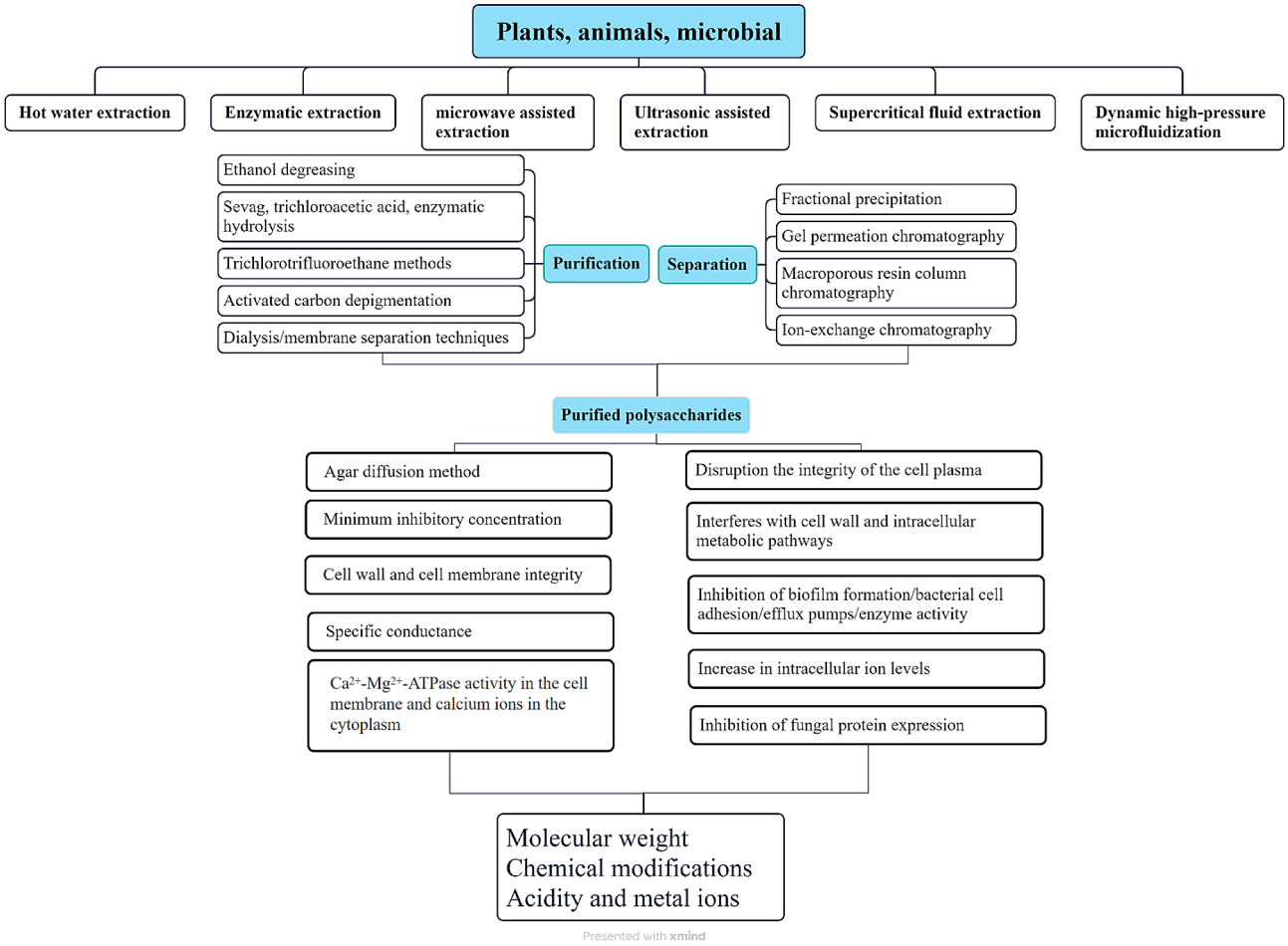

Fig. 1 Isolation and purification of polysaccharides, antibacterial methods, antibacterial mechanisms, and influencing factors

Polysaccharide classification

Polysaccharides are polymers composed of glycosidic linkages connecting more than 10 monosaccharides (Wang et al. 2019b). They are vital components of living organisms and have an assortment of biological properties, such as immune-stimulating, anticancer, and antibacterial properties. There are two forms of polysaccharides: Heteropolysaccharides, which are made up of multiple types of monosaccharide molecules, and homopolysaccharides, which are made up of just one type of monosaccharide molecule (Yehia et al. 2021; Wang et al. 2017). Polysaccharides are widespread in plants, animals, microorganisms. Depending on where they come from, they can be separated into three categories: microbial, plant, and animal polysaccharides.

Plant polysaccharides

Starch, cellulose, and pectin, which are commonly found in plants are examples of plant polysaccharides. There are two primary categories of plant polysaccharides: one serves as an energy storage substance in plants and the other is a cell wall polysaccharide used to construct plant tissue (Li et al. 2022b, c). Plant polysaccharides are highly regarded for their safety, non-toxic nature. Most plant polysaccharides demonstrate various biological properties, including antibacterial, antioxidant, immunomodulatory, and health benefits (Liang et al. 2022a; Su et al. 2023; Wang et al. 2022; Yin et al. 2021a, b). Plant polysaccharides from various sources are typically extracted using hot water. The inherent activity of plant polysaccharides is typically low. Most plant polysaccharides have a low intrinsic activity. Nonetheless, chemical changes have the power to enhance or alter polysaccharide activity in bacteria. Examples of such modifications include phosphorylation, sulfation, and selenium incorporation (Chen et al. 2014; Qin et al. 2013; Song et al. 2015).

Animal polysaccharides

Animal polysaccharides represent a class of biomacromolecules with biocompatibility, non-antigenicity, low toxicity, and biodegradability. This category encompasses notable examples instance heparin, chitosan, chitin. Animal polysaccharides can be broadly classified into two categories: one comprises chitin or chitosan, while the other encompasses glycosaminoglycans, including heparin, chondroitin sulfate, hyaluronic acid, and heparan sulfate (Zhao et al. 2015). Polysaccharides extracted from aquatic animals, such as abalone, have attracted considerable attention owing to their abundance, distinctive structure, advantageous physical and chemical properties, ease of extraction (Xiong et al. 2020). Polysaccharides derived from aquatic animals exhibit biological activities such as antitumor, antioxidant, and antibacterial properties. These polysaccharides are predominantly found in the skin, muscle, cartilage, viscera of aquatic animals (Li et al. 2016; Xiong et al. 2020).

Microbial polysaccharides

Microbial polysaccharides are carbohydrate polymers that exert protective effects against microorganisms, including bacteria, fungi, and cyanobacteria, during the metabolic processes (Qamar et al. 2022). Examples of microbial polysaccharides include xanthan gum, alginate, and those from *Ganoderma lucidum*, *Flammulina velutipes*, and *Hydrangea*. Microbial polysaccharides are essential to the development of vaccines for preventing infectious illnesses. Various polysaccharide vaccines, including the *Streptococcus pneumoniae* polysaccharide vaccine, have been approved for human use (Abhijit et al. 2012). Research has indicated that microbial polysaccharides can serve as thickeners, stabilizers, emulsifiers in the manufacture of medications. Additionally, they can be used to develop efficient drug delivery systems (Ahmad et al., 2015; Wang et al. 2023a). Microbial polysaccharides include biological actions that include cholesterol-lowering, antimicrobial properties (Song et al. 2023). Based on their morphological location, microbial polysaccharides can be sorted into three groups: intracellular, cell wall, and extracellular polysaccharides (Ahmad et al., 2015).

Polysaccharide extraction, isolation, and purification

Extraction of polysaccharides

The polysaccharide structure possesses numerous hydroxyl groups, rendering it polar, thus soluble in water but insoluble in organic solvents. Various extraction methods for polysaccharides can influence their extraction rates and purities. The strengths and weaknesses of various polysaccharide extraction techniques, along with the factors that affect them, are outlined in Table 1.

Hot water extraction and alcohol precipitation

Polar solvents such as ethanol are commonly utilized for extracting polysaccharides due to their affinity with these polar molecules. Hot water extraction and alcohol precipitation are common methods used for polysaccharide extraction. These methods rely on the principle that polysaccharides are soluble in water but insoluble in ethanol. This process involves immersing the cells in hot water, which leads to their absorption of water and expansion, brought about the breakdown of the cell wall and a decrease in the resistance to mass transfer of the polysaccharides. The crude polysaccharide is initially extracted using hot water, and subsequently, the crude polysaccharide is obtained through precipitation with three times the volume of 95% ethyl alcohol (Niu et al. 2020).

Table 1 Advantages and disadvantages of different polysaccharide extraction methods and influencing factors

Extraction method	Advantage	Disadvantage	Influencing factors of yield	Reference
Hot water extraction	Simplicity and convenience	Long time, high energy consumption	Extraction temperature, extraction time, solid to liquid ratio	Yin et al. (2022); Liang et al. (2021)
Enzymatic extraction	Mild extraction conditions, good repeatability, low energy consumption	High costs and technical requirements	Extraction temperature, extraction time, enzyme concentration, pH	Muneeb et al. (2022); Xiong et al. (2020); Hu et al. (2023)
Microwave-assisted extraction	Strong penetrating power, low cost	High experimental equipment requirements	Microwave power, solvent-to-solid ratio, extractionduraton	Wen et al. (2018)
Ultrasonic-assisted extraction	High efficiency, low energy consumption	It may change the structure and composition change of polysaccharides	Ultrasonic power, solvent-to-solid ratio, extraction duration,	Yan et al. (2021)
Supercritical fluid extraction	Short time consumption, high extraction efficiency	The extraction process is complex	Ultrasound power, pressure, temperature, solvent	Zhao et al. (2021); Dias et al. (2021)
Dynamic high-pressure microfluidization	Straightforward operation, short processing time, high safety	Small interaction chamber, low processing capacity	DHPM pressure, solvent, macromolecule concentration	Zhang et al. 2018); Guo et al. (2020)

The polysaccharide extraction efficiency is impacted by variables including temperature, time, solid to liquid ratio, and number of extraction cycles (Muneeb et al. 2022; Liu et al. 2023). The hot water extraction method is advantageous owing to its simplicity and convenience. However, it has drawbacks such as being time-consuming, extracting polysaccharides from hot water is time-consuming and necessitates high temperatures, which can trigger the maillard reaction and caramelization reaction under such conditions. These reactions can degrade polysaccharides, reducing extraction efficiency. Additionally, excessive temperature or prolonged extraction may alter the functional properties of the polysaccharides (Yi et al. 2020; Wang et al. 2023b).

Employed hot water extraction and alcohol precipitation methods to extract crude polysaccharides from the fruiting bodies of *P. placentodes*, yielding a crude polysaccharide content of 2.20% (Yin et al. 2022). The optimal extraction conditions for *Pomelo* Peel's polysaccharide were as follows: solid to liquid ratio of 34 mL/g, extraction duration of 2 h, two extraction cycles, temperature of 87 ℃, yielded a polysaccharide extraction rate of 8.73% (Juan et al. 2019).The optimum extraction conditions for *Erythronium sibiricum* bulb polysaccharides were a solid to liquid ratio of 37 mL/g, extraction duration of 4.28 h, temperature of 90 °C, three extraction cycles. This resulted in a polysaccharide extraction rate of 37.25% ± 0.17% (Chen et al. 2016a).

Enzymatic extraction

Enzymatic hydrolysis induces cell wall breakage under specific extraction conditions, enzymes facilitate the accelerated release of polysaccharide components, aiding the transfer of polysaccharides into the extract (Das et al. 2021). The most frequently used enzymes are proteases, cellulases, and pectinases (Nadar et al. 2018; He et al. 2022). Protease hydrolysis is a commonly used method to extract polysaccharides from marine organisms. Typically, a protease with low specificity is used to fully hydrolyze proteins. The commonly employed proteases consist mainly of trypsin, papain, and pepsin (Yi et al. 2020). The enzymatic extraction method is relatively gentle and causes less damage to cells, resulting in a higher extraction rate, lower energy consumption, and promising prospects for development (Rostami and Gharibzahedi 2017; Xiong et al. 2020; Muneeb et al. 2022).

The optimal extraction conditions for *Ganoderma lucidum* spore polysaccharides were as follows: solid to liquid ratio of 2:70, temperature of 50 ℃, extraction duration of 150 min, and enzyme concentration of 2.3%, yield a polysaccharide extraction rate of 6.7285% (Mai and Au 2018). The ideal extraction parameters for polysaccharides from *mulberry* leaves were as follows: temperature of 45 ℃, pH 6.5, extraction duration of 50 min, yield a polysaccharide extraction rate of 24.04% ± 0.98% (Yang et al. 2017).

Microwave-assisted extraction

Microwave-assisted extraction utilizes microwaves generated by radiation to induce heating of polar substances within cells. This leads to an increase in the intracellular temperature and pressure generated by vaporization, leading to the rupture of cell walls and cell membranes. This process forms tiny pores through which polysaccharide components are released. The effectiveness of microwave extraction depends on variables examples of microwave power, ratio of solvent to solid, and extraction duration (Zhao et al. 2015). Unlike the hot water extraction and alcohol precipitation methods, microwave heating is initiated within the polysaccharide itself and interacted with the polar solvent. This resulted in uniform heating, thereby enhancing the polysaccharide yield at the same temperature (Vinatoru et al. 2017). The positive aspects of microwave-assisted extraction include strong penetrating power, short time consumption, low cost, and low solvent dosage (Wen et al. 2018).

The ideal extraction parameters for polysaccharides from the pulp and peel of *Algerian jujube* (*Ziziphus Lotus L.*) were as follows: microwave power of 600 W, extraction duration of 40 min, liquid-to-solid ratio of 26.69 mL/g, resulting in an extraction rate of 13.98% ± 1.55% (Berkani et al. 2020). The ideal extraction parameters for *Moringa oleifera Lam.* leaf polysaccharides were as follows: microwave power of 700 W, temperature of 70 ℃, extraction duration of 70 min, solid to liquid ratio of 35 mL/g, resulting in an extraction rate of 2.96% ± 0.11% (Chen et al. 2017).

Ultrasonic-assisted extraction

Ultrasonic extraction harnesses raw energy and solvents to extract compounds from a variety of plant materials. The transmission of ultrasonic pressure waves and cavitation effects enhances the extraction efficiency of the solvents. The breakage of cell walls, triggered by the bursting of cavitation bubbles and the localized generation of high temperatures, facilitates the release of cell contents into the extraction medium. (Ebringerová and Hromádková 2010). Ultrasound offers advantages such as high efficiency, high extraction rate, elevated biological activity of the extracted polysaccharides, short extraction duration, low energy consumption. Nevertheless, the molecular weight and bioactivity of polysaccharides may be altered since ultrasonic treatment (Yan et al. 2021).

The ideal extraction parameters for sunflower tray polysaccharides were as follows: solid to liquid ratio of 1:37, temperature of 52.50 ℃, ultrasonic duration of 31 min, power of 300 W, extraction conducted twice. The ideal extraction parameters for *Arctium lappa L.* root polysaccharides were as follows: power of 158 W, temperature of 50 ℃, solid to liquidratio of 31 mL/g, extraction duration of 83 min, the extraction rate of *Arctium lappa L.* root polysaccharides is 8.22% (Jiang et al. 2019).

Ultrasound-microwave extraction

Ultrasound generates a robust physical force through the cavitation effect but has a limited heating capacity, whereas microwaves rapidly heat the sample but are constrained by mass transfer (Qiu et al. 2022). The ideal extraction parameters for *loquat* (*Eriobotrya japonica*) leaves polysaccharides were as follows: extraction duration of 6.5 min, microwave power of 500 W, ultrasound power of 450 W, the extraction rate of *loquat* (*Eriobotrya japonica*) leaves polysaccharides is 8.22% (Fu et al. 2020). Therefore, ultrasonic and microwave methods are combined to enhance polysaccharide extraction.

Other extraction methods

Supercritical fluid, dynamic high-pressure microfluidization (DHPM)-assisted, and can also be employed for enhance the efficiency of polysaccharide extraction.

Supercritical fluid extraction uses CO_2 as the fluid. Under supercritical conditions, CO_2 efficiently extracts the components. Upon restoring atmospheric pressure, the polysaccharide components dissolved in CO_2 separate from the gaseous fluid, resulting in liquid-state extraction of the polysaccharide (Zhao et al. 2021; Dias et al. 2021). Supercritical fluid extraction is characterized by short time consumption, high extraction efficiency, and promising development prospects. Polysaccharide was extracted from *bamboo* (*Phyllostachys heterocycla*) leaves by supercritical fluid extraction. The ideal extraction parameters comprised a pressure of 40 MPa, temperature set at 50 ℃, duration of 2 h, ethanol volume of 30 mL. The polysaccharide extraction rate was 2.47% (Zou et al. 2018).

DHPM is a developing technology that combines high-pressure impact, intense shear, transient pressure drop, ultrahigh pressure in a synergistic manner (Zhang et al. 2018; Guo et al. 2020). This technique offers benefits such as a straightforward operation, short processing time, and high safety (Huang et al. 2012; Liu et al. 2008). Huang et al. applied DHPM for *Lentinan* extraction. The findings demonstrated that, under the conditions of a liquid-to-solid ratio of 65 mg/mL, DHPM pressure of 147 MPa, temperature of 83 ℃, the extraction rate of *Lentinan* reached 7.20% (Huang et al. 2012).

Polysaccharides could be extracted from *Lentinus edodes* stipe under vacuum. The ideal extraction parameters were: vacuum degree of 0.08 MPa, solid to liquid ratio of 1:26, temperature of 65 ℃, extraction duration of 25 min, and stirring speed of 1200 r/min. The polysaccharide extraction rate was 4.28% (Li et al. 2019). Besides the aforementioned auxiliary extraction methods, polysaccharides could also be extracted using ultrasonic subcritical water conditions (190 W, 140 °C), achieving an extraction rate of 17.34% for *Lentinan* (Zhang et al. 2018).

Isolation and purification of polysaccharides

During polysaccharide extraction, impurities such as proteins, pigments, inorganic salts, nucleic acids, and oligosaccharides are often present, potentially impacting the biological function of polysaccharides. Hence, it's crucial to eliminate impurities to obtain pure and singular polysaccharides for subsequent studies. The removal of polysaccharide impurities primarily involves the elimination of proteins, pigments, and small-molecule impurities (Shi 2016; Muneeb et al. 2022).

Commonly employed protein removal methods include Sevag (Lei 2016), trichloroacetic acid (Lei 2016), the trichlorotrifluoroethane methods (Qu et al. 2013), and enzymatic hydrolysis. The Sevag method is a frequently used laboratory technique for protein removal. The ratio of the polysaccharide solution to Sevag reagent (n-butanol: chloroform = 1:4) was 3:1 (Zhang et al. 2023), and the

mixture was shaken and centrifuged several times until there was no protein separation. This method requires mild conditions and minimizes polysaccharide degradation. The trichloroacetic acid method has low efficiency in removing proteins, and polysaccharides are prone to degradation. Currently, a combination of methods is frequently employed to enhance protein removal efficiency. The protein was removed from polysaccharides of corn mulberry by Sevag and enzymatic method. Pigments can be eliminated by adsorption methods (using activated carbon and diatomite), hydrogen peroxide treatment, decolorization using macroporous resins (Cai et al. 2016; Qu et al. 2013; Zhang et al. 2010). The activated carbon adsorption method is straightforward but results in a high loss rate of polysaccharides, and hydrogen peroxide treatment involves strong oxidation (Chen et al. 2016). Higher concentrations can easily disrupt the polysaccharide structure and affect its bioactivity. The macroporous resin method, which is characterized by fast adsorption, large surface area, and mildness, is a common approach for polysaccharide depigmentation (Duan et al. 2020).

Small-molecule impurities mainly consist of oligosaccharides and inorganic salts, which can be eliminated using a semi-permeable membrane. This method is straightforward and has a minimal impact on polysaccharides; however, it is time consuming and inefficient. After this treatment, further purification is performed to obtain pure polysaccharide (Hu et al. 2023).

Polysaccharides could be precipitated using a graded precipitation method based on their varying solubilities in organic solvents, with ethanol being the most commonly used organic solvent. Common methods employed to purify polysaccharides encompass fractional precipitation, gel permeation chromatography, macroporous resin column chromatography, and ion-exchange chromatography (Liang et al. 2022b).

Employed fractional precipitation to isolate polysaccharides from *Asparagus officinalis*, resulting in three polysaccharides: AOP-4 (40% ethanol), AOP-6 (60% ethanol), and AOP-8 (80% ethanol) (Zhao et al. 2012). Utilized salting-out to isolate polysaccharides by introducing neutral salts (such as NaCl, KCl, $(NH_4)_2SO_4$, etc.) into polysaccharide solutions, exploiting the varying solubility of polysaccharides of different molecular weights in salt solutions of different concentrations (Lei 2016).

Employed ion-exchange chromatography to fractionate Pithecellobium dulce polysaccharides. The unrefined polysaccharide solution underwent elution on a DEAE Sephadex A-25 column for elution, resulting in the isolation of three polysaccharides: PDP-1, PDP-2, and PDP-3 (Preethi and Mary 2016). Macroporous resin chromatography is employed not only to eliminate proteins and pigments from the polysaccharides but also to separate and purify polysaccharides. Yang et al. evaluated four macroporous resins. Among these, the AB-8 macroporous resin proved to be more effective in isolating and purifying tea seed polysaccharides, yielding 18.7% polysaccharides with 89.2% purity (Yang et al. 2015).

Antibacterial methods of polysaccharides

Agar diffusion method and minimum inhibitory concentration (MIC) analysis

The agar diffusion technique stands out as the most frequently employed method for evaluating the antibacterial efficacy of compounds (Zhou et al. 2022). The diffusion capability of the tested substances can affect the accuracy of the experimental results; high molecular weight polysaccharides exhibit poor diffusion in agar. Consequently, the agar diffusion method is unsuitable for determining the antibacterial activity of the tested substances, particularly hydrophobic compounds, and the microdilution method can be employed for assessment (Ren et al. 2014). *Broussonetia papyrifera* fruit polysaccharides exhibited excellent antibacterial efficacy towards *E. coli*, *Bacillus subtilis* (*B. subtilis*), *Pseudomonas aeruginosa* (*P. aeruginosa*), *Staphylococcus aureus* (*S. aureus*). The antibacterial effect increased with increasing concentrations. The MICs were 0.3, 0.3, 0.25, 0.25 mg/mL, respectively (Han et al. 2016). The effectiveness of the polysaccharide derived from lily bulb extract in inhibiting bacterial growth showed a notable increase with dosage (Wang et al. 2019c).

Determination of cell wall and cell membrane integrity

Alkaline phosphatase (AKP) resides between the cell wall and cell membrane, with its activity typically undetectable in the culture medium under normal circumstances (Wang et al. 2018). β-galactosidase is located in the bacterial cell membrane, and the impact of antibacterial drugs on bacterial cell membranes can be assessed by detecting AKP and β-galactosidase. The AKP activity remained unchanged after treatment with polysaccharide from *Chaetomium globosum* CGMCC 6882 (GCP). However, intracellular β-galactosidase activity significantly increased, indicating that the polysaccharide from GCP disrupted the cell membranes, with no significant effect on the cell wall (Wang et al. 2018).

Specific conductance analysis

Alterations in electrical conductivity can indicate variations in cell membrane permeability. After exposure to GCP polysaccharide, the conductivity increased with increasing treatment time. This elevation suggested leakage of ions from the cell membrane (Wang et al. 2018). After treatment with *Cordyceps polysaccharide*, the conductivity of *E. coli* rose in tandem with the rise in β-galactosidase activity. This suggested that this polysaccharides enhance the permeability of the cell membrane,

causing ions to seep out, thereby inhibiting its growth (Zhang et al. 2017b).

Determination of Ca^{2+}-Mg^{2+}-ATPase activity in the cell membrane

Ca^{2+}-Mg^{2+}-ATPase facilitates the transport of Ca^{2+} and Mg^{2+} across the plasma membrane. It hydrolyzes ATP and transports intracellular Ca^{2+} out of the cell, thereby maintaining the intracellular Ca^{2+} levels (Abdulkareem et al., 2019; Wang et al. 2020a). Both low molecular weight polysaccharides (GCP-2) and high molecular weight polysaccharides (GCP-1) isolated from GCP inhibited Ca^{2+}-Mg^{2+}-ATPase in the cell membranes of *E. coli* and *S. aureus*. GCP-2 exhibited stronger inhibition of *E. coli* than GCP-1, and both GCP-1 and GCP-2 showed stronger inhibitory effects on *S. aureus* than on *E. coli* (Zhang et al. 2021).

Antibacterial mechanism of polysaccharides

Polysaccharides primarily exert antibacterial effects by interfering with cellular structure and hindering biological energy metabolism (Wang et al. 2021). However, research on the antibacterial mechanisms of polysaccharides is limited. This review discusses the inhibition of biofilm formation, bacterial adhesion, efflux pump activity, disruption of the plasma membrane and cell wall integrity, interference with intracellular metabolic pathways, disruption of cell membrane proteins, and suppression of fungal protein expression.

Disruption the integrity of the cell plasma membrane

The plasma membrane is exceedingly thin and surrounds the cell surface and is primarily composed of lipids and proteins. It is primarily engaged in the exchange of materials, energy, and information with the external environment, as well as in maintaining the stability of the internal environment. The plasma membrane is a crucial barrier that regulates the flow of cytoplasm in cells, helping maintain normal osmotic pressure. Plant polysaccharides impede bacterial adsorption onto host cells, enhance the permeability of cell membranes, and hinder nutrient transport, thereby exerting bacteriostatic effects (Zhou et al. 2022). The cell wall performs functions such as maintaining cell shape, participating in material transport, and facilitating information transfer. Damage to the cell wall may result in cell death upon exposure to external stimuli.

The alterations in morphology of E. coli subjected to green tea polysaccharide (gTCP) treatment were assessed using scanning electron microscopy and transmission electron microscopy. The findings indicated that untreated *E. coli* displayed the characteristic rod-shaped morphology, whereas the morphology of *E. coli* treated with gTCP underwent significant changes (Zhou et al. 2020). *Armillariella tabescens* mycelial polysaccharides caused shrinkage and damage to *E. coli* cells, leading to the breakdown of cellular structure and morphology, as well as membrane rupture (Zhang et al. 2022). The AKP and β-galactosidase activities remained unchanged in a medium without GCP and *Cordyceps cicadae* polysaccharides but significantly increased in a medium containing GCP and *Cordyceps cicadae* polysaccharides (Wang et al. 2018; Zhang et al. 2017b).

Inhibition of biofilm formation

A biofilm is a complex three-dimensional arrangement enveloped by a matrix of hydrated polysaccharides, proteins, DNA (Jamal et al. 2018; Nandakumar et al. 2015). Biofilms consist of a diverse mix of microorganisms or pathogens, where microbial cells attach to surfaces, both living and non-living. This adhesion is irreversible and difficult to remove. Biofilms are primarily composed of water and EPS layers that consist of polysaccharides, nucleic acids, and proteins. These components crosslink to form a protective layer, rendering bacteria more resistant to human immune responses, antibiotics, and other interventions (Jamal et al. 2018; Vishhwakarma 2019). Biofilm formation encompasses four primary stages: the initial adherence of microbial cells to biotic or abiotic surfaces through appendages or other physical forces, followed by microcolony formation; maturation, structural development of the biofilm; and ultimately, separation of the biofilm (Jamal et al. 2018; Sutherland 2001). Bacterial infections are associated with the formation of bacterial biofilms, as seen in infections caused by foodborne pathogens, such as *S. aureus* and *Salmonella*. Bacteria are more difficult to eliminate in a biofilm than in a wandering state, and biofilm formation is an important reason for the failure of antimicrobial therapy (Nandakumar et al. 2015). Polysaccharides exert antimicrobial effects by influencing biofilm adhesion and inhibiting biofilm population sensing.

Chlamydomonas reinhardtii sulfate polysaccharide (Cr-SP) efficiently dissolved the preformed biofilms, as revealed by extracellular DNA and optical microscopy analyses, indicating interactions with the polymeric components of the biofilm and antibacterial effects (Vishhwakarma et al., 2019). Biofilms are complex structures formed by microorganisms, primarily bacteria, adhering to surfaces. The presence of biofilms complicates bacterial eradication and cleansing processes. Polysaccharides primarily exert their antibacterial effects by hindering cell adhesion and aggregation. Polysaccharides show promising potential for inhibiting biofilm formation and can serve as a natural and relatively benign antibacterial agent. Effective inhibition of biofilm adhesion prevented the binding of foodborne pathogens to the host surface and delayed the biofilm formation.

Inhibition of bacterial cell adhesion

Bacterial cell adhesion is an essential process facilitated by interactions between carbohydrates and proteins, occurring between adhesins on microbial and host cell surfaces (Wittschier et al. 2010). Adhesins are a class of biomolecules found on the surface of bacteria and typically comprise proteins or glycoproteins. A polysaccharide extract (PFSMpe) from the *Pleurotus flabellatus* strain Mynuk exhibited an anti-adhesive effect on foodborne bacteria. The extracellular polysaccharide from the *Pleurotus flabellatus* strain Mynuk demonstrated the highest inhibition of adhesion (>50%) to *Enterococcus faecalis* (Vunduk et al. 2019). The green tea acidic polysaccharide CS-F2 and ginseng acidic polysaccharide with a negatively charged group are vital for the adherence of host bacteria (Lee et al. 2006).

Inhibition of efflux pumps

The presence of efflux pumps is another significant factor in bacterial resistance. Exopolysaccharides produced by *Lactobacillus plantarum* and *Bacillus* impede the efflux pump in *E. coli* ATCC 35,218 biofilms, reduce indole metabolism to restrain the antibiotic resistance of *E. coli* (Mahdhi et al., 2018). Polysaccharides derived from probiotics in the extracellular environment inhibit the proliferation of *E. coli* O157:H7 by suppressing genes related to flagella synthesis and chemotaxis (Kim et al. 2009).

Disruption of cell membrane proteins

Cell membrane proteins, including enzymes and carrier proteins, play crucial roles in maintaining the integrity. Disruption of these proteins can disturb the integrity of the enzyme system within bacterial membranes, ultimately resulting in microbial death (Zhang et al. 2017b).

Inhibition of enzyme activity and increase in intracellular ion levels

Ca^{2+} are pivotal in regulating diverse cellular processes, and their buildup in the cytoplasm can trigger heightened levels of intracellular reactive oxygen species, culminating in cytoplasmic dysfunction and apoptosis (Carraro and Bernardi 2016). Ca^{2+}-Mg^{2+}-ATPase hydrolyzes ATP to transport Ca^{2+} from the cell membrane to the exterior of the cell, thereby regulating the cellular Ca^{2+} levels. This process contributes to the maintenance of cellular stability and function (Abdulkareem et al., 2019). Compared with the group without xanthan oligosaccharide (LW-XG), the activity was significantly decreased in the LW-XG group, facilitated the accumulation of Ca^{2+} in the cytoplasm (Wang et al. 2020a). The polysaccharide of GCP led to the accumulation of Ca^{2+} in the cytoplasm, disrupting the sodium-potassium balance (Wang et al. 2020b).

High iron chelation of polysaccharides

Most polysaccharides possess an anionic charge and chelation of metals could potentially serve as an antibacterial mechanism for polysaccharides (Wang et al. 2021). The hydroxyl and carboxyl groups present in polysaccharides have the ability to chelate metal ions, thereby impeding bacterial nutrient absorption and consequently exhibiting antibacterial activity (Li et al. 2022b, c). Iron is essential for bacterial growth and polysaccharides can hinder bacterial iron uptake by removing it from the environment. Earlier research has demonstrated that chelating agents with a high affinity for iron (III) exhibit antibacterial activity (Shao et al. 2017; Xu et al. 2011; Zhou et al. 2015).

Enteromorpha prolifera degrades polysaccharides (CDPE) through carboxymethylation. CDPE binds to iron through its hydroxyl and carboxyl groups, demonstrating diminished affinity for iron (III) (Shao et al. 2017). *Enteromorpha prolifera* isohydroxamate-degrading polysaccharide (HCDPE) exhibits high affinity for iron (III). Compared to CDPE, HCDPE exhibited enhanced affinity towards *E. coli* and *P. aeruginosa*. Sulfate substitution can augment the chelating and reducing capabilities of compounds containing iron. Abalone polysaccharides, after sulfate modification, were found to hinder the absorption of iron by bacteria (Wang et al. 2019a).

Inhibition of bacterial nucleic acid and protein synthesis

Polysaccharides can bind to bacterial DNA targets and influence bacterial replication, transcription, and translation, thereby inhibiting the synthesis of bacterial nucleic acids and proteins (Wang et al. 2021). Polysaccharides can bind to plasmid DNA and cause it to break down into smaller fragments (He et al., 2010; Belbekhouche et al. 2019). Tea polysaccharides can bind to plasmid DNA, causing a notable degradation effect, characterized by the appearance of thread-like DNA. This suggests that plasmid DNA may be a target for polysaccharides that exert antibacterial effects (Du et al. 2005).

Inhibition of fungal protein expression

Fungal proteins are involved in bacterial metabolism, synthesis, and expression. *Cicada* polysaccharides diminish bacterial virulence by suppressing fungal protein expression. Additionally, GCP polysaccharides hinder the proliferation of *S. aureus* by inhibiting the expression of fungal proteins (He et al., 2010; Wang et al. 2018). Polysaccharides can influence fungal protease activity by modulating the enzyme distribution and conformation, cofactors, and other factors.

Other antibacterial mechanisms

In addition to the antimicrobial mechanisms outlined above, polysaccharides impede DNA and RNA synthesis

and influence folic acid metabolism. The amount of extracellular DNA (eDNA) in the biofilm formation of *Streptococcus*, *Neisseria mucosae*, *B. subtilis* and *E. coli* was decreased by sulfated polysaccharides of *Chlamydomonas rheinissima* (Vishhwakarma et al., 2019). *Tetrastigma hemsleyanum* polysaccharides hindered the activity of 6-phosphofructokinase-1 and suppressed secondary phosphorylation of fructose-6-phosphate. This interference affected glycolysis and gluconeogenesis in *E. coli*, causing insufficient energy acquisition by *E. coli*. Consequently, this led to the inhibition of *E. coli* growth, thereby serving an antibacterial function (Chen et al. 2019).

Factors affecting the antibacterial activity of polysaccharides

The antibacterial effectiveness of polysaccharides is influenced by various factors, such as molar ratio, molecular weight, solubility, chemical bonding, extraction, and chemical modification (Govindarajan and Noor 2021; Jiang et al. 2020; Li et al. 2022a, c; Wang et al. 2021).

Effect of molecular weight on antibacterial activity of polysaccharide

Low molecular weight polysaccharides exhibit more potent inhibitory on bacteria than high molecular weight polysaccharides. Additionally, polysaccharides from the endophytic fungus *Chaetomium globosum* demonstrated a stronger inhibitory effect on *S. aureus* than against *E. coli*. They proposed that low molecular weight polysaccharides may have penetrated the bacterium, thereby exerting antibacterial activity by influencing cell proteins and energy metabolism. The decrease in molecular weight exposed more reactive groups, enhancing diffusion and consequently improving the polysaccharide's bioactivity (Li et al., 2021; Zhang et al. 2022). Polysaccharides (BPPs) from *Broussonetia papyrifera* fruits were employed in bacterial inhibition assays on four bacterial species, employing the agar diffusion method. The findings suggested that BPP-3, characterized by a low relative molecular weight, displayed the highest efficacy in inhibiting the growth of the four tested strains (Han et al. 2016).

Ultrasonic degradation influences the spatial or chemical structure of polysaccharides through cavitation and breaking of mechanical bonds. The antibacterial activity of polysaccharides can be heightened following ultrasonic degradation, possibly due to the decrease in molecular weight and the breaking of intermolecular hydrogen bonds after ultrasonic degradation (Li et al. 2022a, c; Wang et al. 2023b).

Effect of chemical modifications on the antibacterial activity of polysaccharides

Following sulfation, carboxymethylation, sulfonation, acetylation, and other modifications, polysaccharide substituents can be altered, leading to enhanced antibacterial activity. Hydroxylated derivatives of polysaccharides were obtained through carboxymethylation, which enhanced polysaccharide biological activity. Polysaccharides from *Sargassum* and *Enteromorpha prolifera* (DPE) were modified through carboxymethylation and hydroamination, respectively. Antibacterial results indicated that the modified polysaccharide exhibited antibacterial activity, whereas the unmodified polysaccharide did not demonstrate antibacterial activity (Li et al. 2018).

Sulfate acidification enhances the biological activity of polysaccharides. Polysaccharides can enhance bioactivity compared to those not subjected to sulfated acidification, and the introduction of sulfuric acid radicals enhances the capacity of polysaccharides to disrupt the cell walls and cytoplasmic membranes (Fakhfakh et al. 2017; Huang et al. 2007). Sulfated polysaccharides extracted from *Chlamydomonas rheinissima* impede biofilm formation and alter bacterial metabolic processes. This interference resulted in the loss of their ability for normal growth and reproduction, affecting the structure and function of bacteria, and ultimately leading to bacterial death (Vishhwakarma et al., 2019; Jridi et al. 2019).

Sulfonation is an effective means to increase the antibacterial activity of polysaccharides, and its mechanism may involve sulfate groups that intensify the disruption of cell walls and membranes, leading to bacterial death (Li et al. 2016). The antibacterial activity of *Egyptian malt* polysaccharides increased with the increasing precipitation of cetylpyridinium chloride (Fakhfakh et al. 2017).

Effects of acidity and metal ions on the antibacterial activity of polysaccharides

Determined the antibacterial properties of α-chitosan and β-chitosan against *Listeria* using the agar diffusion method (Qian et al. 2015). The findings showed that the antibacterial activities of α-chitosan and β-chitosan decreased with increasing pH, increased significantly with the addition of Co^{2+} and Ni^{2+}, and increased with the addition of K^{+}.

Application of polysaccharide in antibacterial

As drug resistance continues to escalate, there is an urgent need to devise novel antibacterial medications characterized by potent efficacy and minimal susceptibility. Polysaccharides, prevalent in plants, animals, and microorganisms, have attracted considerable interest because of their robust antibacterial capabilities. An *Amikacin capsular* polysaccharide nanoparticle capable of inducing cytosolysis and disrupting cell membranes,

ultimately resulting in cell demise. This nanoparticle exhibited minimal cytotoxicity and excellent biocompatibility (Shi et al. 2023). Polysaccharides serve as effective reducing agents and stabilizers for synthesizing silver nanoparticles with varied biological activities (Yugay et al. 2020). Polysaccharides derived from microalgae are known for their biodegradability, biocompatibility, and cost-effectiveness. A polysaccharide isolated from green microalgae as both a reducing agent and stabilizer in the synthesis of silver nanoparticles. This polysaccharide displayed considerable antibacterial effectiveness, which was dose-dependent (Navarro Gallón et al. 2019). Polysaccharides, being natural macromolecules, originate from various sources, yet their structures are intricate. Despite this, most antibacterial research remains largely theoretical, indicating the necessity for additional exploration and advancement in this domain.

Conclusion

Polysaccharides are intricate macromolecules found abundantly in animals, plants, and microorganisms. Polysaccharides demonstrate diverse biological properties, with their antibacterial capabilities showing potential for clinical use. The extraction, purification, and molecular weight of polysaccharides can impact their biological efficacy. Hence, it is crucial to employ suitable techniques for their extraction, isolation, and purification.

Commonly used methods for isolating and purifying polysaccharides include the Sevag method, macroporous resin column chromatography, fractional precipitation, and ion-exchange column chromatography. Polysaccharides can undergo modifications, including sulfation, ultrasonic degradation, and carboxymethylation to enhance their biological activities. Polysaccharides demonstrate antibacterial properties by impeding biofilm formation, interfering with intracellular metabolic pathways, and disrupting the integrity of plasma membranes and cell walls, and inhibiting fungal protein expression. Polysaccharides are diverse and abundant, which makes it important to study their antibacterial properties. This review encompasses the methodologies involved in polysaccharide extraction, isolation, and purification, along with the factors influencing their antibacterial efficacy and mechanisms. This study establishes a fundamental theoretical foundation for exploring the antibacterial properties of polysaccharides.

Abbreviations

AOP	*Asparagus officinalis* polysaccharides
PDP	*Pithecellobium* dulce polysaccharides
DEAE	Diethylaminoethyl
DHPM	Dynamic high-pressure microfluidization
MIC	Minimum inhibitory concentration
TEM	Transmission electron microscopy
ESEM	Environmental scanning electron microscope
PVC	Polyvinyl chloride
GCP	*Chaetomium globosum* CGMCC 6882 polysaccharides
B. subtilis	*Bacillus subtilis*
P. aeruginosa	*Pseudomonas aeruginosa*
S. aureus	*Staphylococcus aureus*
gTcp	Green tea polysaccharide
Cr	SP-*Chlamydomonas reinhardtii* sulfate polysaccharide
EPS	Lp-extracellular polysaccharides from *Lactobacillus plantarum*
CDPE	*Enteromorpha prolifera* degrades polysaccharides
HCDPE	Enteromorpha prolifera isohydroxamate-degrading polysaccharide
BPPs	*Broussonetia papyrifera* polysaccharides
DPE	*Enteromorpha prolifera*
AKP	Alkaline phosphatase
E. coli	*Escherichia coli*

Acknowledgements

Not applicable.

Authors' contribution

The completion of this review paper was accomplished by the collaboration of all authors. Lihui Liang and Xiaofeng Gao gathered information and wrote the manuscript. Qihang Su, Yu Ma, Shuzhen Zhao and Huanjie Zhang reviewed and provided suggestions for the article. The author(s) read and approved the final manuscript.

Funding

This work was funded by the Henan Province Key R&D and Promotion Special Project (Science and Technology Research, 232102110158), key R&D projects in Henan Province (221111110600), the Henan Provincial Central Leading Local Science and Technology Development Fund Project (Z2022134035), the Xinyang Ecological Research Institute Open Fund (2023XYMS15).

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interest.

Received: 19 February 2024 / Accepted: 2 May 2024
Published online: 11 May 2024

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