

Review

The Interactions of Carbohydrate-Based Biostimulants with Roots: From Perception to Response

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Abstract

In the current context of environmental sustainability and reduced agricultural inputs, biostimulants represent one of the most efficient, eco-friendly and innovative strategies to preserve plants from biotic and abiotic stresses and to ensure sustainable agriculture. Ranging from benefic microorganisms, seaweed extracts, and humic acids to complex carbohydrates such as polysaccharides and oligosaccharides, these biostimulants are able to increase plant growth, photosynthetic efficiency, root development and nutrient uptake when they are applied during seed priming as foliar sprays or as liquid and solid soil amendments. The mechanisms underlying their effective action on plants are mainly related to the enhancement of antioxidant defenses and the regulation of hormonal pathways, particularly auxin homeostasis and transport. Several studies reported the relevance of biostimulant application in promoting root growth. In plants, roots play crucial roles, performing a variety of functions such as nutrients and water uptake, mediating stress perception and adaptation, influencing the rhizosphere microbiome, and providing structural support. The effectiveness and perception of polysaccharide-based biostimulants (PBs) are highly dependent on crucial factors, including the degree of depolymerization and the chemical modifications such as acetylation, methylation, sulfation, and oxidation. Furthermore, not all receptors and co-receptors involved in the recognition of PBs have yet been identified. However, there remain many gaps in our understanding regarding the interaction between biostimulants and roots, which is still far from fully elucidated. For these reasons, the present review provides a comprehensive overview of current research on biostimulants–root interactions, with a particular focus on polysaccharide-based biostimulants. It highlights the mechanisms involved in their recognition by plants roots, from perception to response, and the subsequent signaling cascades and the molecular pathways activated, with special emphasis on existing knowledge gaps and future research perspectives.

Keywords: roots; biostimulants; polysaccharides



Academic Editor: Karin Stana Kleinschek

Received: 30 November 2025

Revised: 12 January 2026

Accepted: 13 February 2026

Published: 24 February 2026

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1. Introduction

In the context of a growing world population and ongoing climate change, agriculture is facing major challenges, particularly due to constraints related to the efficient use of

resources and the reduction in the application of chemical fertilizers and/or pesticides to preserve the ecosystem and human health [1]. Research attempts to find effective and powerful alternatives that can reduce the use of these agrochemicals to guarantee sustainable and ecological agriculture. One of the most promising and environmentally friendly emerging strategies is the use of bioactive substances extracted or derived from a variety of natural sources such as plants, seaweed, microorganisms, and humic substances known as biostimulants. Since their regulation by the European Union (EU 2019/1009), biostimulants have been gaining more attention and becoming more valued on the economic market due to their interesting biological potential in relation to diverse crops in terms of enhancing physiological processes, and improving plant growth, crop productivity and tolerance against abiotic stressors [2].

In this regard, numerous polysaccharides, corresponding to complex carbohydrates, are potent plant biostimulants and elicitors (e.g., pectin, cellulose, alginate, chitosan, carrageenan, and laminarin). They play vital roles in plants' primary metabolism, acting as signaling molecules that regulate multiple biological processes. They modify the physiochemical characteristics of soil to enhance nutrient assimilation and activate stress tolerance mechanisms, including structural support to the cell wall, ion homeostasis, and stomatal closure [3,4]. These positive effects on plants may differ based on several factors, such as the dosage, the timing and the method of application (foliar spray, soil amendment or both), as well as chemical structure and composition [2]. In recent years, several studies have focused on the physiological potential of polysaccharides and their derivatives (i.e., oligosaccharides and low-molecular-weight fractions) biostimulants (PBs), and the underlying mechanisms involved in plant–biostimulant interactions. However, many unknowns remain, potentially due to their heterogeneous composition.

In this review, we provide a comprehensive overview of recent advances on polysaccharides- and oligosaccharides-based biostimulants and their biological potential to modulate physiological traits, with a particular emphasis on root systems, which play an important role by ensuring anchorage, and water and nutrient uptake, and maintaining interactions with soil microorganisms [5,6]. Owing to their structural diversity, plant roots are a crucial organ and a great model for exploring how these biostimulant molecules influence plant growth.

In addition, we highlight the interactions of exogenous polysaccharide with roots, and the molecular mechanisms underlying their perception as well as signal transduction. We also discuss how chemical modifications of these carbohydrate polymers can impact their biological activity and their recognition by plant receptors, and conclude with future research perspectives.

2. Carbohydrates Act as Stimulants of Plant Physiology

2.1. Mono- and Disaccharides as Cellular Signals

The beneficial impact of carbohydrates on root development or on whole plant growth was initially suggested in 1992 and has since been thoroughly examined in *Arabidopsis* seedlings [7]. Knowing that polysaccharides are long chains of monosaccharides linked by glycosidic bonds, it is essential, before exploring their impact on plants and on their physiological parameters, to understand the biological effect of the monosaccharides and/or disaccharides alone.

The activity of root meristematic cells are highly affected by glucose in a concentration-dependent manner [8,9]. At low concentrations, glucose increases the progression rate of the meristematic cell differentiation, leading to an increase in root length, while at high concentrations, it reduces the auxin levels by repressing the accumulation of the auxin transporter (PIN1), causing a decrease in the size of the meristems (Figure 1) [10].

Glucose, considered a hormone-like signaling molecule, modulates plant growth and development [10], enhances the root vitality, and promotes seedling growth [11]. Gupta et al. [12] reported in *Arabidopsis* that glucose acts synergistically with brassinosteroids (BR) to regulate 72% of genes involved responses to both abiotic and biotic stresses, as well as growth and development. Also, glucose targets kinase proteins and transcription factors, such as MYB75/PAP1, ATR1, MYB28, and JAF13, which can regulate multiple hormonal biosynthetic pathways in plants [9]. Glucose was found to be involved in the upregulation of genes involved in cytokinin (CK) metabolism and signaling, including *ARR6*, which is involved in abiotic stress responses, and *ARR8* expressed via the plant's root and impacts lateral root numbers [13].

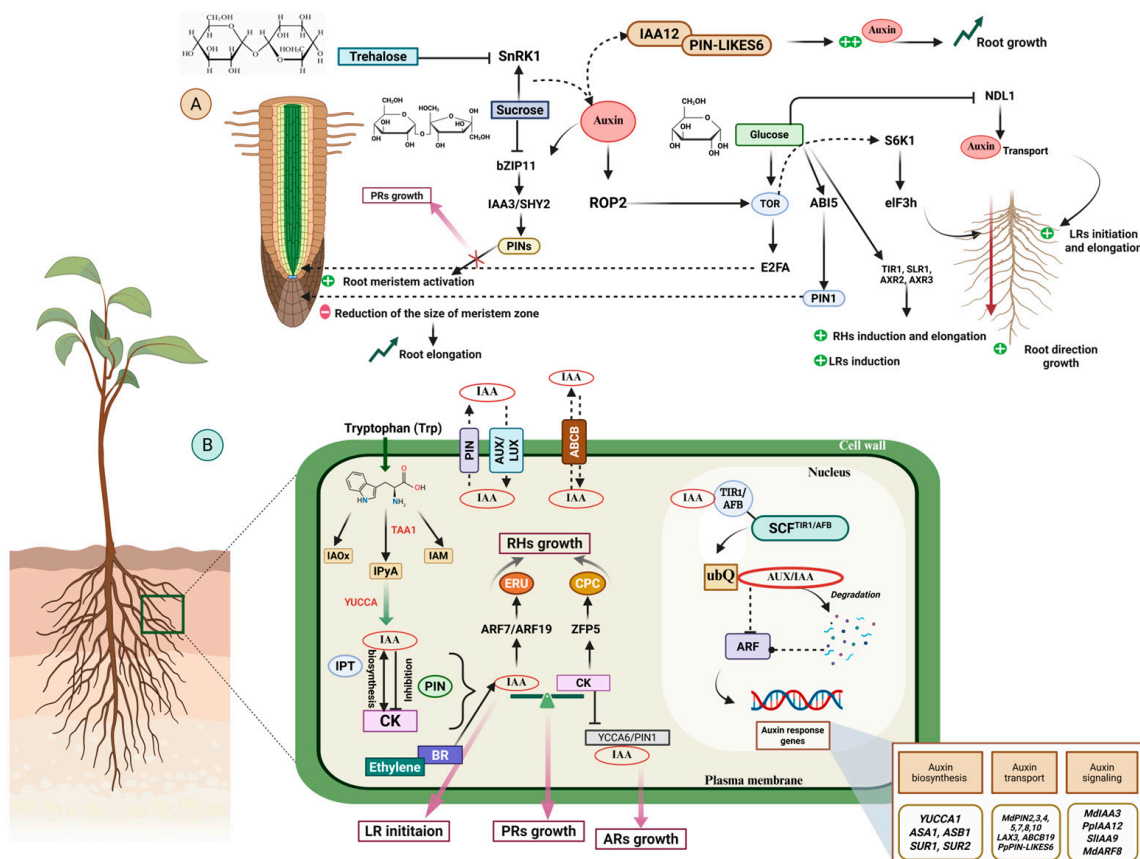


Figure 1. (A) Schematic diagram of sugar–auxin interactions and how they control root growth. (B) Model of synthesis, transport of auxin and its crosstalk with other phytohormones to induce root growth, Created in BioRender. AHCHOUCH, F. (2026) <https://biorender.com/q4nlh9p>, accessed on 10 November 2025. ABCB, ATP-binding cassette subfamily B; ABI5, abscisic acid insensitive5; AFB, auxin signaling F-Box protein; ARF, auxin-responsive transcription factors; ARs, adventitious roots; AUX/LAX, auxin influx transporters; AXR, auxin resistant; BR, brassinosteroids; CK, cytokinin; CPC, CAPRICE; E2FA, E2F transcription factor A; ERU, ERULUS; IAA, indole-3-acetic; IAM, indole-3-acetamide; IAOx, indole-3-acetaldoxime; IPT, isopentenyl transferases; IPyA, indole-3-pyruvic acid; LR, lateral roots; NDL1, n-myc down regulated like1; PIN, PIN-FORMED; PRs, primary roots; RHs, root hairs; ROP2, Rho-like GTPase from plants 2; SCF, SKP1-Cullin-F-box complex; SLR1, solitary response 1; SnRK1, sucrose non-fermenting 1-related protein kinase 1; TAA1, tryptophan aminotransferase of Arabidopsis 1; TIR, transport inhibitor response; TOR, target of rapamycin; Trp, tryptophan; ubQ, ubiquitin; ZFP, zinc finger protein.

In the plant model *Arabidopsis thaliana*, Sairanen et al. [14] reported that sucrose, a disaccharide composed of fructose and glucose, led to an upregulation of multiple indole-3-acetic acid (IAA) biosynthetic pathways via the phytochrome-interacting factor (PIF)

family of transcriptional regulators, which has been shown to be involved in the regulation of various aspects of plant growth. Lalonde et al. [15] hypothesized that exogenous sucrose is absorbed with water by the root via the xylem then it is transported through the leaf apoplast to the phloem, ultimately acting as an endogenous molecule. Pasternak et al. [7] reported that the addition of exogenous carbohydrates plays an important role as a direct source of carbon needed for the synthesis of organic molecules (e.g., amino acids, nucleotides, and hormones) involved in seedlings growth. They found that sucrose upregulates the level of PIN1 and induces the transcription factors of auxin's pathway, preventing the RAM (root apical meristem) size and primary root growth [7]. These findings are aligned with those reported by Agrawal et al. [16], confirming that sucrose induces the transcription of the auxin response factor (ARF) and lateral organ boundaries domain (LBDs) genes, via the target of rapamycin (TOR) pathway, leading to a development of primary and lateral roots. For example, sucrose induces the ARF7 expression, which activates the auxin signaling pathways as a result the initiation of lateral roots' development. Zhang et al. [17] show that, under the treatment of a moderate concentration of exogenous sucrose, the growth and the number of lateral roots (LRs), as well as the overall volume and surface area of peach (*Prunus persica*) roots, significantly increased. These results are attributed to the promotion of the auxin synthesis related genes (*PpYUC2* and *PpYUC6*), auxin transport-related genes (*PpPIN1*, *PpPIN2* and *PpPIN3*) and the stimulation of SnRK1 protein kinase activity (sucrose non-fermentation-1-protein kinase 1), thus leading to an accumulation of auxin in the root system, and hence controlling their growth [17]. Trehalose, a disaccharide composed of two glucose units, has an inhibitory effect on SnRK1, whereas sucrose counteracts this repression and activates SnRK1. This activation, in turn, promotes the auxin synthesis, the expression of auxin transporter genes, and interaction with two proteins participating in auxin signaling pathways, IAA12 repressor and PIN-LIKES6 transporter, leading to an accumulation of auxin and ultimately enhancing root growth and development [17].

Both glucose and sucrose can stabilize N-MYC DOWNREGULATED-LIKE 1 (NDL1), a cytoplasmic effector which interacts with the G β γ dimer (heterotrimeric G protein with β and γ subunits) to promote *Arabidopsis* primary root growth and lateral root formation by modulating auxin transport [18]. In maize, LeClere et al. [19] confirmed the correlation between the concentration of indole-3-acetic acid (IAA), sugar content (glucose and sucrose), and the upregulation of auxin biosynthesis genes, such as *ZmYUC* (a kernel-specific maize homolog of the flavin monooxygenase YUC), via the hexokinase-mediated pathway.

Mono- and disaccharides act on several hormone pathways, given that plant hormones regulate numerous metabolic pathways and play a crucial role in regulating root development and root system architecture (RSA) formation. Among them, auxins are important for root development from the cellular level to the level of the whole root system [20]. Cytokinins reduce cell elongation and subsequently root elongation [21], and gibberellins promote cell production in the root meristem and cell expansion in the root's elongation zone [22]. Auxin can interact with these hormones (Figure 1) to control the development and growth of the plant's root.

2.2. Root Growth: Impact of Sugar and Hormone Signaling

The auxin signaling network is modulated by sugars at several levels (Figure 1A). They regulate the transcription of important auxin-related genes, such as auxin receptors (TIR1 and ABP1), repressors (AUX/IAA), and auxin-responsive transcription factors (ARFs), as well as the accumulation of auxin carrier proteins on the plasma membrane. Through the small GTPase ROP2, auxin activates TOR Kinase, which may be regulated by glucose. TOR plays a crucial role in phosphorylation of some targets associated with

cell cycle, translation, lipid synthesis, N assimilation, and ABA (abscisic acid) signaling. The phosphorylation of the E2FA transcription factor by TOR activates it and binds to the promoters of cell cycle genes, leading to the activation of the root meristem. In parallel, TOR phosphorylates S6K1 and eIF3h thereby promote the directional growth of plant roots. Glucose activates ABI5 (ABSCISIC ACID INSENSITIVE 5), a bZIP family member, which reduces the accumulation of PIN1, limiting the auxin flux to the meristem and subsequently reducing the primary root meristem size [10]. A reduction in meristem size increases the rate of cell differentiation, causing cells to leave the primary root meristem and enter the elongation zone, which ultimately enhances root elongation. Glucose promotes root length, and the initiation and elongation of lateral roots and root hairs by mediating auxin signaling components, including an F-Box TIR1 (TRANSPORT INHIBITOR RESPONSE 1), a SOLITARY RESPONSE1 (SLR1), and AUXIN RESISTANT 2 and 3 (AUX2 and AUX3) [23]. Glucose affects the stability of N-MYC DOWNREGULATED LIKE 1 (NDL1) protein, which forms a complex with G β γ dimers disrupting auxin transport causing local auxin maxima in roots regulating lateral root initiation and elongation [13]. In parallel, sucrose inhibits the transcription factor bZIP11, playing a crucial role in controlling and regulating primary growth via the modulation of auxin signaling and transport. bZIP11 induces the expression of IAA3/SHY2, a repressor of auxin transport, and decreases the auxin transporter PIN-FORMED (PIN) expression, which restricts polar auxin transport to the root tip and, as a result, auxin stimulates primary root growth [24].

Indole-3-acetic acid (IAA) is biosynthesized from its major precursor, 1-tryptophan (Figure 1B). Trp-dependent pathways include the indole-3-acetaldoxime (IAOx), indole-3-acetamide (IAM), and indole-3-pyruvic acid (IPyA) pathways by TAA1 and YUCCA. Regarding those pathways, the IPyA is regarded as the primary contributor to IAA synthesis [25]. The AUX1/LAX1 and ABCB proteins transport IAA, which is then exported to the cytoplasm by PIN. In the nucleus, auxin causes the ubiquitination and degradation of Aux/IAA proteins via SCFTIR1/AFB. The degradation of the Aux/IAA repressor restores ARF activity, allowing for the transcription of auxin-responsive genes to proceed [26]. For lateral roots' (LRs') growth, auxin promotes their development by increasing RPH1 (leaf rust resistance gene) expression via ARF7, which is an auxin response factor, and via LBDs, which refers to a lateral organ boundary domain. Auxin favorably enhances root hairs (RHs) through an ERU-dependent pathway (ERULUS is a key regulator of RHs growth). ZFP5 (zinc finger 5) induces the transcriptional level of CAPRICE (CPC), a MYB (myeloblastosis) protein, which links to the promoters implicated in RHs patterning [27]. In the root apex, auxin and cytokinin have an antagonistic relationship; CKs regulate positively the auxin biosynthesis by the transcriptional control of specific auxin genes (CYP79B2/B3 and NIT3), while auxin acts as a repressor of CK biosynthesis through the downregulation of IPT genes (ISOPENTENYL TRANSFERASES) [28]. The balance between these two hormones controls the primary root development [21]. Low concentration of ethylene and the presence of brassinosteroids promote lateral roots' initiation respectively, by increasing Trp-dependent auxin biosynthesis and auxin transport in the meristem [29].

2.3. Polysaccharides-Based Biostimulants

Over the past decade, the term biostimulant has emerged to designate formulated products composed of natural compounds, substances, and/or microorganisms that, when applied to plants either via roots drench, foliar spray, or a mix of both, is designed to stimulate and promote natural mechanisms in the plant, by enhancing nutrient use efficiency, increasing tolerance to abiotic and biotic stresses, and ultimately improving crop yield and quality without causing long-term adverse effects on the environment or plant health [30]. Colla et Rouphael [31] proposed nine categories of biostimulants: humic and

fulvic acids [32], chitin and chitosan derivatives [33], seaweed extracts (brown, red and green macroalgae) [34], complex organic materials (from agro-industrial waste) [35], inorganic salts including phosphite [36], protein hydrolysates and free amino acids [37], beneficial chemical elements (Al, Co, Na and Si) [38], kaolin and polyacrylamide [39], and arbuscular mycorrhizal fungi, plant growth-promoting rhizobacteria PGPR and beneficial fungi like *Trichoderma* spp. [40].

Natural plant biostimulants (PBs) represent an important and sustainable tool to replace and reduce the use of chemical inputs in modern agriculture. The definition of PBs has been established under the new European regulation (EU) 2019/1009, which defines plant biostimulants as follows: “a plant biostimulant means a product stimulating plant nutrition processes independently of the product’s nutrient content, with the main aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: (a) nutrient use efficiency, (b) tolerance to abiotic stress, (c) quality traits, or (d) availability of confined nutrients of the soil or rhizosphere” [41].

Among the classes of biostimulants, polysaccharides have attracted a particular interest in agriculture, due to their non-toxicity, biodegradability, eco-compatibility and biological efficiency [42]. Due to their versatile physicochemical characteristics and their ability to be modified both physically and chemically to enhance their properties, polysaccharides have attracted growing interest across various fields and numerous applications, particularly in agriculture. They play crucial roles in plant primary metabolism, providing structural support to the cell wall, and also act as signaling molecules that regulate multiple biological processes [3]. Numerous polysaccharides and their oligomers are potent in plants’ immunity and as biostimulants in different plant species (Table 1). They act as elicitors by stimulating the plant’s defenses, improving crop yield and plant vigor, and increasing the uptake of soil nutrients and seed germination, providing a longer shelf life for fruits and protecting plants against several abiotic and biotic stresses [34,43]. Although they have been largely reported to have positive effects on plant physiology, due to that fine status, it has to be noticed that their effects largely depend on different parameters, such as the dose, the mode of application, the plant tissue, the plant species and even probably the genotypes within a specific plant species, and they may have negative effects on the overall plant physiology [44].

It is crucial to distinguish a plant elicitor from a plant biostimulant. A biostimulant can have beneficial effects on growth, development, and resistance to abiotic stress, as well as on crop yield and quality, regardless of its nutrient content [45], whereas an elicitor is a substance that stimulates any type of plant defense, promoting secondary metabolism to protect the cell and the entire plant [46]. So, a biostimulant can improve natural physiological plant functions, and an elicitor can activate plant immunity, which depends on the physiological state of the plant. However, biostimulants are not plant elicitors or inducers of resistance against biotic stress [47], while an elicitor can be a biostimulant because there can be an overlap between the stimulation of defense mechanisms induced in response to typical biotic stress and those involved in plants’ responses to abiotic stress [48] and growth. For example, oligo-carrageenans enhanced defense against pathogens via JA (Jasmonic acid), SA (Salicylic acid) and ET (Ethylene) pathways and through the target of rapamycin (TOR)-dependent pathway [49]. When the TOR-dependent pathway is activated, it up-regulates the expression of genes related to photosynthesis, C, N and S assimilation and the enzymes implicated in the phenolic compounds’ production, leading to the promotion of the growth of the plant [49]. Fungal β -glucan and laminarin have an elicitor activity against pathogens but are also capable of increasing cytosolic Ca^{2+} concentration [48]. Free cytosolic Ca^{2+} correlates to many physiological stimuli including light, salinity, drought, phytohormones and abiotic stresses [48]. In addition, it is well known that Ca^{2+} can me-

diates many cellular processes involved in plant growth and development [50]. Moreover, as mentioned previously, an elicitor can induce the SA and JA defense pathways. The salicylic acid (SA) not only functions against pathogens but also influences plant growth and development [51], and it can regulate IAA biosynthesis and transport [52]. Jasmonic acid (JA) is widely used in regulating disease resistance against necrotrophic pathogen, but it can crosstalk with the auxin signaling pathways by inducing the expression of auxin synthase gene (ASA1), which regulates the biosynthesis of auxin and further promotes root growth [53]. So, the differentiation between biostimulants and elicitors is very tricky to state because their actions could be linked to the cell signaling pathways induced in response to the molecules, but also to the membrane receptors involved in the perception of their ligand.

Table 1. The biostimulant activities of the most-used polysaccharides.

Biostimulant Activities	Polysaccharides	Target Plants	References
Root growth	Cellulose (β -D-glucopyranose with β -1,4 glycosidic bonds)	Tomato	[54]
	Oligo-alginates (DP2 to DP6) (α -L-glucuronic acid (G) and β -D-mannuronic acid (L) with β -1,4 or α -1,4 glycosidic bonds)	Rice and Carrots/Maize/Rice/ <i>Brassica camp</i> L./Wheat	[55–60]
	Ulvan (Neutral sugar (L-rhamnose D-xylose and D-glucose), and glucuronic and iduronic acids, connected by β -1,4 or α -1,4 glycosidic bonds)	Maize/ <i>Arabidopsis</i> /Mung bean/ <i>L. esculenta</i> /Sprouts	[61–65]
	Oligo-galacturonic acid (OGA) (α -1,4-linked galacturonic acid)	Alfalfa/Pea/Cucumber/Sugar beet/Soybean	[66–70]
	Chitosan (β -(1,4)-D-glucosamine)	<i>Zizania latifolia</i> /Pepper/Potato	[71–73]
Nutrient efficiency	Bacterial cellulose Oligo-alginates (DP2–3) Chitosan	Tomato	[54] [74] [33]
Germination rate	Cellulose (CNF) Oligo-alginates (1445 Da) Chitosan	Spinach Maize Maize	[75] [56] [76]
Abiotic stress tolerance	Cellulose Oligo-alginates (DP2–3) Ulvan Chitosan	Wheat/Spinach Wheat and Tomato <i>L. esculenta</i> Grapevine/Vegetable Crops/Maize	[75,77] [74,78] [63] [79,80]
	Cellulose	Sesame/ <i>Artemisia absinthium</i> /Spinach	[75,81]
Plant quality traits	Oligo-alginates	Wheat/Tomato	[74,78]
	Carrageenan (sulfated galactan) (D-galactose and 3,6-anhydro-D-galactose with β -1,4 or α -1,4 glycosidic bonds)	Tobacco/ <i>Pinus radiata</i> /Eucalyptus Trees/Tobacco/Maize	[82–86]
	Ulvan	<i>Arabidopsis</i> /Mung Bean/Sprouts	[62,64,65]
	Oligogalacturonides	Tomato/Soybean	[65,70,87]
	Chitosan	Tomato/Orchids/Basil	[88–90]

3. Polysaccharides-Based Biostimulants Involved in Root Growth: Perception and Cell Signaling

When applied to the soil, PBs are directly in contact with plant roots and interact with root cells through specific receptors (plant RLKs receptors). Plant PRRs are localized on the cell's surface, typically receptors-like kinases (RLKs) or receptors-like proteins (RLPs),

which can recognize a wide range of microbes or plant-derived molecules [91]. The PRRs detect MAMPs (microbe-associated molecular patterns) or DAMPs (damage-associated molecular patterns), leading to the activation cascades of immune responses through calcium-dependent protein kinases (CDPKs), ROS burst, calcium (Ca^{2+}) influx, callose deposition, hormone signaling and mitogen-activated protein kinase (MAPK) [92]. The MAPK cascades are essential for transferring the signal from the PRRs to the nucleus, where the activation of transcription factors take place, helping with the regulation of the expression of defense genes [91].

RLKs are involved in the regulation of plant development and root growth, as well as in the response to biotic and abiotic stresses by facilitating intracellular communication [93,94]. They are composed of a single transmembrane domain, an extracellular region that recognizes and binds to signaling molecules, and an intracellular kinase domain, which is activated after the recognition mechanism, modulating a variety of cellular responses [94,95]. Based on the variety of their extracellular domains, we can classify RLKs into diverse subfamilies, including leucine-rich repeat RLKs (LRR-RLKs) and lysin motif domain RLKs (LysM-RLKs) [96]. The LysM family is classified into LysM-containing receptor-like kinase (LYK) and LysM-containing receptor-like proteins (LYP) [97]. LYKs are crucial in plant–pathogen interactions by mediating innate immunity in plant species [97].

Depending on their regulation of processes in plants, studies have divided the RLKs into two subgroups: RLKs associated with plant growth, such as ACR4/CLV1 (lateral root initiation), PSY1R (cell division) and MARIS (RHs growth), and RLKs associated with plant immunity, including CERK, OsCEBIP and CORK [93,94,97,98]. Still, a considerable number of RLKs are not fully characterized.

3.1. Alginates

Several studies have confirmed the beneficial effects of algal extracts on root architecture and nutrient uptake, specifically seaweed polysaccharides, such as alginate [99]. The biostimulant action of these macromolecules is linked to the activation of distinct signaling pathways triggered by diverse metabolites, including hormone-like substances, carbohydrates, vitamins, polyamines, carotenoids, amino acids, betaines and phenols [99].

Alginate and its oligosaccharides derivatives are one of the most explored algal polysaccharides in terms of biostimulation. Spraying algal oligosaccharides with a DP (degree of polymerization) of 20 prepared by the chemical depolymerization of native polysaccharides on tobacco plants: (i) alternate α -1,4 and β -(1,4)-sulphated galactan (Poly-Gal) obtained from red algae *Schizymenia binderi*, (ii) β -(1,4) linked mannuronic acid (Poly-ManA) and (iii) α -(1,4) guluronic acid (Poly-GulA), both obtained from Chilean marine macroalgae [100]. They reported that these fractions stimulate growth and defense activities. These results rely on the activation of the antioxidant enzyme ascorbate peroxidase (AP), which modulates the level of antioxidant substances ASC (ascorbate) and DHA (dehydroascorbate), which, in turn, regulate plant growth [100]. Moreover, they confirmed that Poly-ManA and Poly-Gal showed the highest increase in the physiological parameters of the plant, such as height and weight of fresh tissue. The contrast between the three fractions is suggested to be linked to the bond β -(1,4), whereas the Poly-GulA responds as the control-treated plants.

Due to its chemical structure with the presence of carboxyl groups, thermal stability and binding potential to carbon compounds, alginate can create a polymeric network increasing soil structure and aeration, stimulating root growth and the soil microbiome, which is the main producer of enzymes, while acting as a slow-release fertilizer [101,102]. AOSs (alginate oligosaccharides) generated by the degradation of alginate have been studied for their active effects on root growth. AOSs were found to induce the formation of

nitric oxide (NO) in the root system of wheat (*Triticum aestivum* L.), which promotes the formation and elongation of roots by upregulating the gene expression of the TaMPK6 gene, resulting in the activation of nitrate reductase (NR) [103]. Recent studies demonstrated that NO acts as a messenger and mediates the auxin-induced adventitious roots (AR) and influences the auxin signaling via the S-nitrosylation of the TIR1 auxin receptor; hence it promotes root primordial initiation and mediates root growth and development [104,105].

The application of an exogenous AOS enhanced the biosynthesis and transport of gibberellic acid (GA3) and indoleacetic-3-acid (IAA) to the root. Also, it increased the accumulation of sucrose by inducing the activity of sucrose synthase (SS) and sucrose phosphate synthase (SPS) [59]. Zhang et al. [60] reported that AOSs impacted auxin homeostasis and activated auxin signaling pathways, leading to the activation of gene expression: OsYUCCA1 and OsYUCCA5, which boost IAA production in tissues, and OsIAA11 and OsPIN1, which facilitate the IAA transport to the roots, resulting in the enhancement of rice root growth. Moreover, AOSs caused the release of Ca^{2+} from extracellular and cytosolic sources to cytosol to activate nitrogen metabolism, promoting the growth and development of plant tissues [106]. Ca^{2+} is a universal signal molecule that plays an important role in plant growth by regulating root morphogenesis via mediating phytohormones [107]. It has been reported that Ca^{2+} can mediate the signaling of various hormones, specifically auxin, to regulate primary root growth [107]. This signal molecule is involved in the auxin-controlled maintenance of the quiescent center (QC) of roots by regulating PIN1-mediated auxin transport. The modification of Ca^{2+} levels leads to an increase in the auxin accumulation in the QC of the root tip as well as the activation of QC cell division and elongation, ultimately promoting root growth [108]. These results provide a broader understanding of AOSs' effects in the regulation of plant root growth.

For the receptors implicated in the recognition of AOS by the plant cells, Peng et al. [109] suggested that alginate oligosaccharides bind to cell surface receptor AtCERK1, which interacts strongly with these oligo-alginates (Figure 2). Zhang et al. [110] confirmed that AOS activities are extremely dependent on the degree of depolymerization, which modulate the AOS-mediated modulation of phytohormones in wheat: at DP 4 and 3, JA and SA were highly induced, CK and ABA were highly accumulated at DP6, and IAA and GB (gibberellic acid) were expressed at DP5. So, as a result, they suggested that AOS fractions with a DP ranging from 4 to 6, can maximize defense-related hormones (ABA, JA and SA) without compromising growth hormones (IAA and GB). Even for the perception, they suggested that the recognition of oligomers depends on the DP. CERK1 can bind strongly to AOS with a DP 4–6; however, for short AOSs (DP2–3), it is possible that CERK1 would not be engaged in this perception at all and could interact with other receptors. This hypothesis requires further investigation to better understand and clarify the relationship between the structure of oligomers, as well as the impact of the length chains, chemical modification and the degree of depolymerization on their perception by the receptors, and consequently how this impacts their biostimulant/elicitor activities.

3.2. Carrageenans

Another seaweed extract used to stimulate growth in plants is carrageenan. It is extracted from red seaweeds and can promote plant development by regulating metabolic pathways such as photosynthesis, cell division, the synthesis of purines and pyrimidines, as well as the assimilation of nitrogen and sulfur [111]. For the chemical structure, carrageenans are linear polysaccharides of sulfated D-galactose residues linked alternatively by α -(1,4) and β -(1,3) bonds, with different positions of sulfates [112]. For example, lambda carrageenan is composed of three sulfate groups for each disaccharide unit; kappa and

iota carrageenans, respectively, have one and two sulfate groups with an anhydrogalactose bridge [113].

Oligo-kappa-carrageenan (κ OC of molecular weight 10kDa) helps pine trees (*Pinus radiata*) to produce IAA and gibberellins (GA3), which are vital hormones regulating development, elongation, differentiation, and cellular division, and which also enhance root elongation, specifically in the elongation zone of the plant roots [86,114]. In addition, the OC kappa stimulates carbon (C), nitrogen (N) and sulfur (S) assimilation, which are implicated in plant growth [86,115]. This oligosaccharide increases the activity of ribulose 1,5 biphosphate carboxylase/oxygenase (RuBisCO), which in turn plays a crucial role in carbon assimilation by reducing the CO₂ to C and incorporating it into three carbons sugars, serving as source of energy. Also, it enhances the activities of the glutamine synthetase (GlnS) and glutamate dehydrogenase (GDH), playing a vital role in the reduction in nitrate to nitrite, then to ammonium, which are assimilated into glutamine and glutamate, serving as a primary amino acids donor in plant metabolism and as a signaling compounds [86].

It was reported that oligo-kappa-carrageenans was more effective and active than the non-depolymerized carrageenan in tobacco plants growth [115]. Among oligo-kappa-carrageenans, OC with a DP 6 has the most efficient elicitor activity compared to DP from two to ten [116]. This confirms the importance of the DP in biostimulation/elicitation, especially the recognition mechanisms through receptors.

Castro et al. [84] reported that these OCs increase the quantity of total ascorbate (ASC), the ascorbate peroxidase (AP) and glutamate dehydrogenase activities involved in nitrogen assimilation, basal metabolism and cell division in tobacco plants. Increasing AP and ASC levels may influence the carbon fixation in chloroplasts [84] and enhance cell cycle progression and mitosis [117], thereby promoting plant growth. Interestingly, the level of transcripts encoding cyclins A, D and cyclin-dependent protein kinases (CDK) A and B is increased, suggesting an acceleration and/or an activation of cell cycle and, consequently, of cell division [84]. In the plant model *Arabidopsis thaliana*, these cyclins play an important role in root growth by guiding cells via the different successive stages (G1/S/G2/M) of the plant's cell cycle [118]. Research has indicated that oligo-kappa-carrageenans with 20 galactose units sulfated at C4 and linked to an anhydrogalactose improve plant growth such as in the roots by regulating phytohormone synthesis, including IAA, gibberellic acid and trans-zeatin through the activation of the TRR/TRX system (thioredoxin reductase/thioredoxin). The TRR/TRX system is involved in regulating phytohormones levels in plant cells, including auxin, and increasing C, N and S assimilation [85,86,116]. A recent study reported that kappa OCs and oligo-ulvans enhanced the rosette diameter and length of the primary root of *Arabidopsis thaliana* by increasing the level of transcripts encoding enzymes such as RuBisCO, glutamine synthase (GlnS) and enzymes involved in gibberellin A3 synthesis. These results suggest that these oligosaccharides stimulate growth by increasing the expression of genes involved in primary metabolism, phytohormones synthesis and cell division [119].

In tobacco plants, Munoz [83] tested three fractions of OCs (kappa, lambda and iota) obtained by chemical hydrolysis, and an increase in physiological parameters was confirmed when these fractions were applied at two different concentrations; however, the most significant increase was observed with oligo-kappa-carrageenan. Pettongkhao et al. [120] confirmed that sulfated kappa carrageenan has the highest elicitor potential, unlike the desulphated one.

These results show that the use of these three fractions, which share the same molecular weight and have identical glycosidic bonds, (α -(1,4) and β -(1,3)), but differ by the position of the sulfate groups within their chemical structure, leads to a different effect on both growth and pathogen defense. We can hypothesize that those differences are

attributable to the functional groups attached to the saccharide's backbone, such as methyl, carboxyl and, in this case, sulfates. Furthermore, the type of glycosidic linkage itself can play an important role in the recognition by the receptor. Moreover, since sulfated kappa carrageenan exhibited the most interesting results and contains only a single sulfate group on its chemical structure, unlike iota (two sulfates) and lambda (three sulfates), this may suggest that the number and the position of sulfate groups could influence the perception of these molecules by cell membrane receptors, by modulating charge distribution and electrostatic or steric interactions. In this case, further investigation is required to understand the impact of functional groups and their positions (e.g., sulfates) on the plant's receptor recognition and signaling.

González et al. [115] mentioned that the potential plasma membrane receptors associated with the perception of the oligo-carrageenan and the signaling pathways have not yet been identified. It is possible that these molecules can interact with a specific receptor structurally related to TLR2 and/or TLR4 or with another receptor protein kinase (Figure 2), which has still not been identified. So, more studies of the perception of these oligosaccharides are required to further elucidate the receptors and co-receptors involved in this recognition and their mode of action with regard to biostimulation.

3.3. Chitosans and Chitin

Several studies have investigated the potential of chitosan as biostimulant, including its improvements of plant growth, yield, and nutrient uptake, and microorganisms associated with plant roots when used in a small quantity as seed coating agent, foliar spray or as culture substrate incorporate, but [33] research studies have consistently found that chitosan has a negative effect on root growth. The inhibitory effect is probably dose dependent, since low doses of chitosan (0.001 to 0.005%) had no deleterious effect on root development, whereas chitosan treatment at 0.01% reduced total root length by around 15% [121]. It has been reported that the impact of chitosan on root growth is dependent on its mode of application, dose, formulation and frequency [122]. High chitosan concentrations of 100 ppm were shown to substantially inhibit root growth and the total root length fresh weight was approximately 80 to 90% lighter than those of the control [123]. To explain this inhibition of root growth, Lopez-Moya et al. [124,125] showed that treating tomatoes with chitosan suppresses the expression of the homeodomain transcription factor WOX5 and AQC1 (*Arabidopsis* Quiescent Center 1), two key regulators of meristematic cell division [124,125]. It also upregulates the expression of genes involved in the auxin biosynthesis pathways (*YUC2*, *AAO1* and *AMI1*), while downregulating the expression of auxin efflux genes *PIN1*, leading to an accumulation of auxins in the meristems, causing a discontinuity in elongation [124,125]. This allows us to conclude that the cessation of root growth can be activated via auxin signaling pathways.

For the perception of chitosan oligosaccharides (COS), it has been reported in the model plant *Arabidopsis thaliana* that the recognition relies on a complex formed by LysM-RLKs (Lysin Motif Receptor-like kinases) (Figure 2), AtLYK1/CERK1 (LysM-RLK1/CERK1), AtLYK4 and AtLYK5, with a strong affinity for AtLYK5 [126]. In grapevines, the PRRs VvLYK1-1, VvLYK1-2, VvLYK-4 and VvLYK-5 have been demonstrated to perceive COS [126]. However, VvLYK5-1 is more specific to the N-acetyl-D-glucosamine of chitin than to the D-glucosamine without any sulfated groups of chitosan oligomers [126]. In rice, the LysM-RLK OsCERK1 and the LYM proteins OsCEBIP, OsLYP4 and OsLYP6 have been reported for the chitin oligosaccharides perception [127–129]. AtLYK1 and AtLYK4 bind to chitin, leading to a transfer of extracellular signals, activating the downstream pathway of resistance to pathogen attacks [130]. In another study, they reported an interaction between LYK8 and CERK1, forming a receptor complex essential for the activation

of symbiosis signaling by chitoooligosaccharides [131]. Gubaeva et al. [132] reported that chitin is “sandwiched” between the two OsCEBiP receptor units, binding them through hydrogen bonding and hydrophobic interactions mediated by its acetyl groups. In addition, completely deacetylated chitosan was inactivated and failed to trigger a response, confirming that the increase in the degree of acetylation (DA) increases the activity of chitosan and subsequently improves the recognition between the chitin receptor and the molecule [132]. Thus, an increase in the DA and DP can increase the activity of these polysaccharides, emphasizing their key role in the perception and bioactivity of polysaccharides biostimulants.

3.4. Celluloses

To the best of our knowledge, very few studies have been reported on the biostimulant effect of cellulose on root growth. Cellulose application in the soil shows an influence on the rhizosphere enzymatic activities [133]. An anionic hydrogel based on oxidized cellulose nanofibers was tested on sesame seedlings with different carboxyl groups contents (0.7 mmol/g and 1.5 mmol/g). They confirmed that the hydrogel containing 0.7 mmol/g of carboxyl groups has the highest germination rate, longer roots, and greater fresh weight compared to the control (with non-oxidized CNF (cellulose nanofibrils)) and the hydrogel with 1.5mmol/g of carboxylates [134]. This suggests that introducing an appropriate amount of carboxyl groups on chemical structure of cellulose nanofibers enhances their physicochemical characteristics, thereby improving their biostimulant potential, making them a promising candidate for agriculture uses [134]. These findings demonstrate that chemical modification of polysaccharides, such as oxidation, can play a key role in improving their performance as biostimulants and strengthening their interactions with plant cells. Therefore, further studies are required to better understand how the increase in carboxyl group content enhances cellulose properties and how these functional groups interact with plant cells, and even their perception by plant receptors.

The application of cellulose is more directed toward the elicitor activity against pathogen infections. Squire et al. [135] reported that the infiltration of cellulose nanocrystals (CNC) in *Arabidopsis thaliana* reduces the level of infection by the pathogen *Pseudomonas syringae* up to 65%, confirming the use of CNC as an immune primer. Cellulose oligomers have been suggested as DAMPs in plant immunity, mimicking cell wall damage, thus inducing defense responses, oxidative bursts, the augmentation of free cytosolic Ca^{2+} and the expression of PR genes [136,137].

Zarattini et al. [138] reported that the degradation of plant cell wall polysaccharides by microbial LPMOs (lytic polysaccharide mono-oxygenases), a novel family of cell wall-degrading enzymes, cleaving (1,4)-glycosidic bonds of polysaccharides, such as cellulose, led to the release of native and oxidized cello-oligosaccharides (at C1 and C4) of a variable degree of polymerization, from two to ten. They confirmed that these oxidized cello-oligosaccharides (AA9-COS) are perceived as DAMPs and are recognized by plant LRR/RLKs, namely, SIF2/4, BAK1 and THE1, leading to an accumulation of phytoalexin camalexin, to an induction of genes related to SA and JA responses, to callose deposition, and to phytohormones accumulation [138]. In addition, these oligosaccharides modulate positively the sugar importers (SUC and STP) and induce an inhibition of SWEET efflux carriers (sugars will eventually be exported transporters) involved in the export from the cytoplasm to the apoplast, as a strategy to retain intracellular sugars in the cytoplasm to mitigate pathogen attacks [138]. The oxidized cello-oligomers with a DP2 were the most effective, confirming again the important impact of DP on polysaccharides' bioactivities. Given these results, this raises more questions: does the position of oxidation play a role in the biological activity of oxidized polysaccharides? What are the exact signal cascades

implicated in plant growth after recognition of oxidized polysaccharides? Further studies are required to clarify these aspects and answer these questions.

Gandhi et al. [137] suggested that the perception of cello-oligomers with 2–7 glucose residues by CORK1 (CELLO-OLIGOMER-RECEPTOR KINASE 1), a functional leucine-rich repeat-malectin receptor kinase, which is expressed in the vascular tissue of the upper part of the root, may function also as a co-receptor for the perception of mixed linked β -1,3/1,4 glucan oligosaccharides. They identified two other LRR-malectin receptor kinases: *At1g56130* (IGP2/3) and *At1g56140* (IGP4) (Figure 2), which can perceive cello-oligomers or mixed linked glucan oligosaccharides in the apoplast of the cells root. Moreover, CORK1 can recognize the structure of sugars with β -(1,4)-bonds. The study demonstrated that the cello-oligomers induce $[Ca^{2+}]_{cyt}$ elevation, ROS production, plasma membrane depolarization, and WRKY30/40 transcription factor expression, which responds to pathogen attack. Fungal-derived cello-oligomers can be recognized by CERK1, serving as a co-receptor or signaling hub for cello-oligomers' perception [139].

Tseng et al. [140] suggested that CORK1 induced cellulose synthase phosphorylation, and the regulation of cell wall integrity (CWI)-related genes, such as genes involved in biosynthesis of cell wall material, secondary metabolites, and tryptophan. Also, the intensity of the response is dependent on the oligomer's length. Cellotriose (CT) has been identified as the most active cello-oligomers in *Arabidopsis thaliana*. Regarding the secondary metabolites, the study shows that JA is a target of cello-oligomers by upregulating the expression of lipoxygenases involved in JA biosynthesis and by moderating a balance of the JA level in the cell [140].

After the activation of CORK1 by cello-oligomers, the glutamic acid, glutamine, and asparagine levels are upregulated [137]. Glutamine (Gln) is the first organic nitrogenous molecule synthesized in the plant cell and plays a crucial role in plant metabolism, growth and development, and is one of the amino acid present in hydrolysate plant-based biostimulants [37,141]. It reported that glutamine promotes primary root growth and it induces lateral root initiation in *Arabidopsis* seedlings by repressing the IAA12 and IAA14 repressors and activating the transcriptional factors ARF5 and GATA23, which are known to mediate embryo axis formation, vascular development, and lateral root priming and initiation [141]. In addition, there is a hypothesis that Gln metabolism affects indirectly auxin biosynthesis. As is already known, Trp is a precursor of IAA, and the Gln plays a role as an N-donor for the Trp biosynthesis and induced Trp biosynthetic genes *ASA1* and *ASB1*, leading to an increase in Trp levels and contributing to IAA biosynthesis at the lateral root initiation sites [141].

Tseng et al. [140] suggested that there is an interaction between CORK1, BRASSINOSTEROID INSENSITIVE 1-ASSOCIATED RECEPTOR KINASE (BAK1) and FERONIA (FER) (Figure 2). BAK1 is the co-receptor of many PRRs, and it participates in ROOT GROWTH FACTOR RECEPTOR 1 (RGFR1) and RGFR5 signaling, so it mediates roots' meristem development. FER is an *Arabidopsis thaliana* receptor kinase in *Arabidopsis thaliana*, which can regulate a broad range of processes on a cellular and molecular level to ensure plant growth and to incur tolerance against stresses when activated by the peptide ligand, the rapid alkalization factor (RALF) [137,142].

3.5. Oligogalacturonides

Oligogalacturonides (OGAs) derived from pectin can be regulators of root growth and development; however, most of their known activities involve them tending to act as elicitors. Zhao et al. [69] demonstrated that OGAs promote defense genes' expression and limit pathogen infection in plant roots. Gamir et al. [143] revealed that the application of OGAs on the root tissues of plants accumulate ABA, SA, JA and secondary metabolites, including

flavonoids and alkaloids. It is interesting to note that OGAs have a dose-dependent effect: when applied at low concentrations, they can control plant growth, but at high doses, they trigger immune responses in the plant [144].

OGAs can regulate growth and development by an auxin-antagonistic activity [145]. In *Arabidopsis*, auxin-induced genes, including *IAA5*, *SAUR16* and *SAUR-AC*, were inhibited by the application of OGAs; however, no inhibition effect was observed for SA, JA and ethylene [144]. In addition, the antagonist relationship between OGAs and auxin has no impact on the TIR1/AFB receptors and AUX/IAA repressors, concluding that OGAs may act downstream of AUX/IAA, potentially at the promoter regions of auxin-responsive genes [145].

Another important element is in relation to chemical modifications: research studies have shown that methyl esterification reduces the elicitor potential of OGAs, while acetylation inhibits the formation of pathogen in wheat leaves and enhances protection against a root rot pathogen in pea plants [144]. Benedetti et al. [146] reported that the oxidation of OGAs at the C1 position, converting galacturonic acid into galactaric acid, significantly reduced the biological activity of these molecules. Moreover, Liu et al. [142] reported that oxidation or methylation can perturb the capacities of OGAs to bind RALF (rapid alkalization factors) such as RALF1 and RALF23, which regulate FERONIA (FER) and its co-receptors, promoting a multitude of essential processes involving in growth and plant immunity. Degli Esposti et al. [144] suggested that the activity of the OGAs is highly dependent on their chemical structure, functional groups, extraction method used, etc.; however, these parameters make difficult the understanding of their recognition by plants' receptors and the link between a specific OGA and a plant response.

Understanding the mechanisms of the perception of OGAs is necessary to comprehend their role in plants. Studies indicate that all-associated kinases (WAKs) (Figure 2) are the candidates for this perception in *Arabidopsis*, due to their high ability to interact and bind with OGAs and polygalacturonic acid [145]. WAKs were the first identified RLKs linking the plasma membrane to the cell wall by binding pectins, pectic polysaccharides and oligogalacturonic acids [147]. WAK1 has an N-terminal pectin-binding domain, which can be linked to OGAs [148]. WAK1, 2, 3, and 5 are expressed in green organs, and WAK2 is also expressed in a plant's roots, organ junctions, abscission zones and meristems [148,149]. OGAs control downstream signaling, which includes the phosphorylation of MAPK3 and MAPK6, calcium-dependent protein kinase (CDPK) activation, and Ca^{2+} influx [147].

The extracellular domains of WAK1 and WAK2 bind the OGAs of DP 9 to 15 with a much higher affinity over longer pectin polymers [149]. Still, the exact molecular mechanisms involved in the recognition of different DP of OGAs by plant cells remain unclear [150]. Moreover, a recent study reported that none of the WAKs (WAK1 to WAK5) were involved in OGAs' perception for immune activation and the mechanisms involved in this activation remain to be characterized [151]. Degli Esposti et al. [144] suggested that WAKs can participate in a larger regulation of the plant's overall responses, even though they might not be engaged in every OGA-mediated event, and the perception may include several mechanisms, rather than a single receptor. As mentioned previously, the activity of OGAs depends highly on their structure/DP, but the mechanisms behind this recognition need to be fully elucidated.

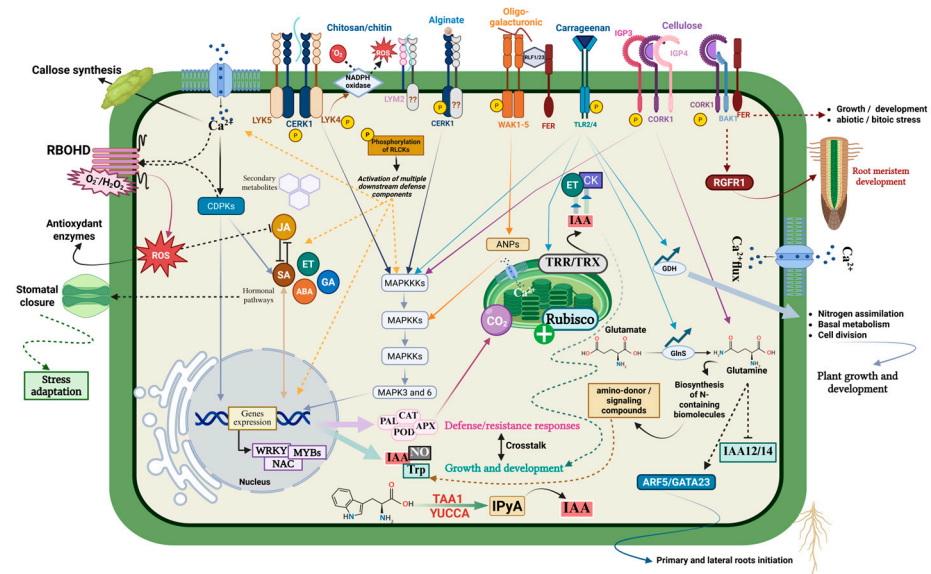


Figure 2. A global overview of PBs, from perception to physiological response [4,92,95,98,128,132,138–140,142,151–157], created in Biorender. AHCHOUGH, F. (2025) <https://BioRender.com/xf038xk>. **Perception:** LYK, LysM-receptor like kinase; CERK1, chitin elicitor receptor kinase; WAK, wall-associated kinase; CORK1, cellulose oligomer receptor kinase1; RLF, RALF (rapid alkalization factor); IGP3, integrity of growth promotion 3; BAK1, BRI1-associated kinase 1; FER, FERONIA. **Signaling cascades:** ANPs, *Arabidopsis* NPK-like protein kinases; RBOHD, respiratory burst oxidase homolog D; MAPKs, mitogen-activated protein kinase; CDPKs, calcium-dependent protein kinase; JA, jasmonic acid; SA, salicylic acid; ET, ethylene; ABA, abscisic acid; GA, gibberellic acid; ROS, reactive oxygen species; RGFR1, root growth factor receptor 1; MYBs, myeloblast transformation transcription factor; CAT, catalase; PAL, phenyl alanyl ammonialyase; POD, peroxidase; APX, ascorbate peroxidase; NO, nitric oxide; Trp, tryptophan; IAA, indole-3-acetic acid; IPyA, indole-3-pyruvic acid; CK, cytokinin; TRR/TRX, system thioredoxin reductase/thioredoxin; GlnS, glutamine synthetase; and GDH, glutamate dehydrogenase.

4. Conclusions and Future Directions

Over the last decade, the use of diverse biostimulants in agriculture has gained more interest and has evolved over the years. Polysaccharides are one of the most-used classes for plant biostimulation and/or elicitation, due to their cost effectiveness, their biodegradability, non-toxicity and eco-compatibility, helping to reach the concept of sustainable agriculture. The elicitor effect of these polysaccharides against biotic stresses is well documented on several crops, at multiple levels, as well as the activation of signaling cascades. However, for biostimulation, the mechanisms involved at the cellular and molecular levels are not yet fully elucidated. In addition, studies have confirmed that there will always be an overlap between the stimulation of typical biotic stress mechanisms and plant responses to abiotic stress and growth [48]. This demonstrates that biostimulation and elicitation may not be completely distinguished, and one relies on the other.

Several studies have shown that the effectiveness of these polysaccharides-based biostimulants highly depends on their degree of depolymerization and chemical modifications (acetylation, methylation, sulfation and oxidation). Thus, this raises more questions that need to be clarified with further future research: after modifying the chemical structure of these polysaccharides (e.g., alginate, cellulose, chitosan, carrageenan, and polygalacturonic acid), how are they perceived by PRRs on plants? Do they penetrate the cells when degraded? What are the motifs of functional groups involved in this perception? How can the addition of certain functional groups affect the biological activity of these biostimulants? Do the receptors remain the same for both unmodified and chemically modified polysaccharides? Or are other receptors

and/or co-receptors added? Do the signaling cascades remain the same after the recognition by PRRs? And what are these exact cascades?

Moreover, studies have confirmed the perception of these polysaccharides-based biostimulants as DAMPs by plant receptors, and these ones do not specifically belong to the subgroup of the RLKs associated with plant growth, but they are classified into the RLKs involved in immune response. This makes us wonder how immune response-specific receptors can generate an effect on root growth and improvement of plants traits, which leads to future research that examines how precisely these PBs, acting as DAMPs, may contribute to systemic and hormonal signaling in plants, despite the complexity of the DAMP signaling network. In addition, not all polysaccharide receptors have been identified, which is considered as a challenging topic in the field and requires further investigations.

At the soil level, many gaps remain in understanding how exactly these PBs, applied as soil amendments, interact with the root system, considering the compartment of soil–microorganisms–root symbiosis. Moreover, root exudates can contribute to the formation of exopolysaccharides by rhizosphere bacteria using a high variety of sugars, including glucose and sucrose [158]. These molecules are a complex composition forming a 3D matrix containing polysaccharides [159]. Understanding the communication between plant roots and these exopolysaccharides is crucial to elucidate how their interaction contributes to the enhancement and promotion of root growth. Similarly, such interactions and mechanisms may also be involved in the perception of exogenous polysaccharides used as biostimulants in soil.

We conclude that there are great opportunities to conduct studies aimed at understanding the mechanisms of action of polysaccharide as biostimulants at different levels (cellular, molecular and phenotypic).

Author Contributions: Conceptualization, F.-Z.A., A.B., A.B.-S., C.D. (Céline Dupuits), S.M., J.R. and C.D. (Cédric Delattre); methodology, F.-Z.A., A.B., A.B.-S., C.D. (Céline Dupuits), S.M., J.R. and C.D. (Cédric Delattre); investigation, F.-Z.A.; writing—original draft preparation, F.-Z.A.; and writing—review and editing, A.B., A.B.-S., C.D. (Céline Dupuits), S.M., J.R. and C.D. (Cédric Delattre). All authors have read and agreed to the published version of the manuscript.

Funding: This research received no external funding.

Institutional Review Board Statement: Not applicable.

Data Availability Statement: The data presented in this study are available within this manuscript.

Acknowledgments: The authors have reviewed and edited the output and take full responsibility for the content of this publication. The schematic representation in the graphical abstract was created in BioRender. AHCHOUGH, F. (2026) <https://biorender.com/ulz1w1j>, accessed on [28 November 2025].

Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

ABA	Abscisic acid
ANPs	Arabidopsis NPK-like Protein kinases
AOS	Oligo-alginates
APX	Ascorbate peroxidase
ARF	Auxin response factor
ASA	Auxin synthase
ASC	Ascorbate
BRs	Brassinosteroids
CAT	Catalase
CDPK	Calcium-dependent protein kinase
CERK	Chitin elicitor receptor kinase

CK	Cytokinins
CNC	Cellulose nanocrystals
CNF	Cellulose nanofibrils
CORK1	Cellulose oligomer receptor kinase1
COS	Oligo-chitosan
CT	Cellobiose
CTOS	Oligo-chitin
CWI	Cell wall integrity
DA	Degree of acetylation
DAMPs	Damage-associated molecular patterns
DHA	Dehydroascorbate
DP	Degree of polymerization
ET	Ethylene
GA	Gibberellic acid
GDH	Glutamate dehydrogenase
GlnS1	Glutamine synthetase 1
IAA	Indole-3-acetic acid
IAM	Indole-3-acetamide
IAOx	Indole-3-acetaldoxime
IPT	Isopentenyl transferases
IPyA	Indole-3-pyruvic acid
JA	Jasmonic acid
LBDs	Lateral organ boundaries domain
LRs	Lateral roots
LYK	LysM-receptor-like kinase
MAMPs	Microbe-associated molecular patterns
MAPK	Mitogen-activated protein kinase
NDL1	N-Myc downregulated-like1
NO	Nitric oxide
OC	Oligo-carrageenan
OGA	Oligogalacturonides
PAL	Phenyl alanyl ammonialyase
PBs	Plant-based biostimulants
PDR9	Pleiotropic drug resistance transporter
PIF	Phytochrome-interacting factor
POD	Peroxidase
PRRs	Pattern recognition receptors
PRs	Primary roots
RAM	Root apical meristem
RBOHD	Respiratory Burst Oxidase Homolog D
RGFR1	Root growth factor receptor 1
RHs	Root hairs
RLF	RALF (Rapid alkalinization factor)
RLKs	Receptors-like kinases
RLPs	Receptors-like proteins
ROS	Reactive oxygen species
RSA	Root system architecture
SA	Salicylic acid
SLR1	Solitary response 1
TIR1	Transport inhibitor response 1
TOR	Target of rapamycin
Trp	Tryptophan
TRR/TRX	System thioredoxin reductase/thioredoxin
ZFP5	Zinc finger 5

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