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REVIEW

Physiologia Plantarum

Glycomolecules: from "sweet immunity" to "sweet biostimulation"?

I. Boulogne[1,2] | **C. Mirande-Ney**[1] | **S. Bernard**[1] | **M. Bardor**[1] | **J.-C. Mollet**[1] | **P. Lerouge**[1] | **A. Driouich**[1]

[1]Université de Rouen Normandie, Normandie Univ, GlycoMEV UR 4358, SFR Normandie Végétal FED 4277, Fédération NORSEVE (Normandie-Québec), Innovation Chimie Carnot, IRIB, GDR CNRS Chemobiologie, RMT BESTIM, Rouen, France

[2]ECOTERCA - ÉCOlogie TERrestre CAribéenne, Université des Antilles, Faculté des Sciences Exactes et Naturelles, Pointe-à-Pitre Cedex, France

Correspondence
I. Boulogne,
Email: isabelle.boulogne@univ-antilles.fr

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Abstract

Climate changes and environmental contaminants are daunting challenges that require an urgent change from current agricultural practices to sustainable agriculture. Biostimulants are natural solutions that adhere to the principles of organic farming and are believed to have low impacts on the environment and human health. Further, they may contribute to reducing the use of chemical inputs while maintaining productivity in adverse environments. Biostimulants are generally defined as formulated substances and microorganisms showing benefits for plant growth, yield, rhizosphere function, nutrient-use efficiency, quality of harvested products, or abiotic stress tolerance. These biosolutions are categorized in different subclasses. Several of them are enriched in glycomolecules and their oligomers. However, very few studies have considered them as active molecules in biostimulation and as a subclass on their own. Herein, we describe the structure and the functions of complex polysaccharides, glycoproteins, and glycolipids in relation to plant defense or biostimulation. We also discuss the parallels between sugar-enhanced plant defense and biostimulation with glycomolecules and introduce the concept of sweet biostimulation or glycostimulation.

1 | INTRODUCTION

In the current context of environmental pollution and climate changes, natural systems, human health, and agricultural production are badly affected (Brevik et al., 2020; Raza et al., 2019). Indeed, environmental pollution is a worldwide ecological challenge due to, among other factors, the extensive use of synthetic chemical pesticides and fertilizers. These synthetic substances have been used since 1945 to reduce plant pests and increase agricultural productivity. However, their intensive usage has generated detrimental consequences for the environment and agricultural production, such as soil erosion, groundwater pollution, river eutrophication, excessive water use, and the development of weeds and diseases resistant to chemical control mechanisms. This usage has also generated a negative impact on human health with poisonings and their related illnesses, for example (Brevik et al., 2020).

Moreover, climate changes are dramatically increasing with more droughts, floods, high temperature variations, and storms. These events have direct, indirect, and socio-economic effects on agricultural production. Indeed, morphological, physiological, and phenotypic changes in plants have direct effects in the form of a decrease in plant productivity. The impact of heat, flooding, and drought on plant productivity is mediated by their indirect effects on soil fertility, water availability, sea level, and the prevalence of foreign pests. Altogether, these effects on plant productivity increase costs, trade, dietary insecurity, and unequal food distribution. Estimates today suggest that more than 50% of agricultural production loss is caused by abiotic stresses (Raza et al., 2019).

The fact that phytosanitary products are widely discredited, together with the need to increase productivity in adverse environments, has recently brought plant biostimulants to the forefront (du Jardin et al., 2020). Biostimulants are natural-based solutions that adhere to the principles of organic farming and are believed to have low impacts on the environment and human health. Thus, they could contribute to reducing the use of chemical inputs. In addition, biostimulants contribute to a circular economy because several of them come from organic waste or co-products from other industries for example (du Jardin et al., 2020; La Torre et al., 2015).

For over a decade, interest in biostimulants and related literature has increased tremendously (du Jardin et al., 2020), leading to a growing world market of 10–15% per year. In addition, a recent European Union regulation (EU 2019/1009), effective in 2022, established the rules relating to the provision of European fertilizers, including biostimulants. In this context, a broad definition of biostimulant is a formulated substance and microorganism that "stimulates plant nutrition processes independently of the product's nutrient content, with the sole aim of improving one or more of the following characteristics of the plant or the plant rhizosphere: nutrient use efficiency and availability of confined nutrients in the soil or rhizosphere; tolerance to abiotic stress; or quality traits" (European Union regulation 2019/1009). Nutrient-use efficiency (NUE) is important in evaluating crop-production systems. NUE not only characterizes the plant's ability to take up nutrients efficiently from the soil but also depends on internal transport, storage, and remobilization of nutrients to increase yield. Consequently, NUE is a function of soil nutrient availability, plant nutrient uptake, and plant nutrient assimilation. NUE depends on several factors, including plant species, environmental conditions, and microorganisms associated with plant roots (Salim and Raza, 2019). Abiotic stresses—such as drought, freezing, high temperature, salinity, chilling, and flooding—significantly affect plants' growth and productivity. These stresses often disrupt the ionic equilibrium, production of reactive oxygen species (ROS), dysfunction of membranes, changes in metabolism and enzymatic activity, and inhibition of photosynthesis (Yang et al., 2009; Negrão, Schmöckel and Tester, 2017).

By scientific consensus, biostimulants comprise five main categories: humic substances, amino acids and protein derivatives, non-nutritive inorganic molecules, microorganisms, and land-plant and algal extracts (du Jardin, 2015; Van Oosten et al., 2017; Yakhin et al., 2017). Several of these biostimulants are enriched in glycomolecules and oligomers of all these molecules. Glycomolecules, e.g., mono-, oligo-, polysaccharides, glycolipids, and glycoproteins, are abundant in nature. They have important roles in primary metabolism, specifically in structural support, and function as signaling molecules controlling many biological processes of organisms (Coté et al., 2008), including plants (Chaliha et al., 2018; Trouvelot et al., 2014). Moreover, glycomolecules from algae, microorganisms, or plants represent sustainable solutions in agriculture because they are biodegradable, biocompatible, nontoxic, biologically active, and quite affordable (Khan et al., 2009). However, only a few studies, mainly focusing on seaweed carbohydrates (Goñi et al., 2020), have described them as active biostimulants. Therefore, it is necessary to comprehensively understand the mechanisms responsible for the biostimulant activity of glycomolecules.

This review article emphasizes complex polysaccharides, formally named glycans, glycoproteins, and glycolipids. The three are referred to as glycomolecules hereafter. They are synthetized by different organisms including bacteria, fungi, seaweeds, and land plants (Table 1). Herein, we focus on glycomolecules from bacteria, fungi, algae, and land-plant origins exhibiting biostimulant activity. We also review a parallel of the concept of sweet immunity. Indeed, many glycomolecules, endogenous or exogenous, are known to be involved in plant immune responses and to counteract biotic stresses (Trouvelot et al., 2014). These elements will allow us to know if, like sweet immunity, a sweet biostimulation or glycostimulation concept could also emerge. Finally, we propose a hypothetical mode of action for land-plant glycomolecules, one of the most promising but least studied categories.

2 | GLYCOMOLECULES AND BIOSTIMULANTS: OCCURRENCES IN LITERATURE

2.1 | Polysaccharides

2.1.1 | Bacterial polysaccharides

The most prevalent bacterial polysaccharides are extracellular, exo-polysaccharides (EPS), and capsular polysaccharides (CPS). Interestingly, some bacterial strains also synthesize unexpected polysaccharides for prokaryotes such as cellulose, alginate, and fructans like inulin and levan (Coté et al., 2008; Robyt, 1998). EPS consists of carbohydrates, mainly in the α-pyranoside form, and are organized in an amorphous layer surrounding the bacterial cell or are secreted outside into biofilms. They may be further organized into another structure, the CPS (Yates et al., 2021). EPS are composed of homopolysaccharides like α-D-glucans, β-D-glucans polysialic acid, etc. (Figure 1) and heteropolysaccharides like xanthan, gellan, fructans, wellan, rhamsan, etc. (Figures 2 and 8; Nwodo et al., 2012). CPS are diverse classes of high-molecular-weight polysaccharides produced by both gram-negative and gram-positive bacteria, which have similar structures and properties as EPS (Ovodov, 2006).

EPS isolated from *Pseudomonas entomophila* PE3 applied on sunflower seeds (*Helianthus annuus* L.) stimulated growth and stress resilience under saline-field conditions (Fatima and Arora, 2021). Another study showed that EPS from *Bradyrhizobium* sp. IC-4059 coated on seeds of pigeon peas (*Cajanus cajan* (L.) Millsp.) enhanced plant volume, nodulation, seed yield, and protein content and stimulated the growth of indigenous soil rhizobia (Tewari et al., 2020). Nonetheless, very few studies are available on bacterial EPS as biostimulants. However, several studies on EPS-producing bacteria, species like *Pseudomonas aeruginosa*, *Azotobacter vinelandii*, *Sphingomonas paucimobilis*, *Azotobacter* sp., *Paenibacillus* sp., *Klebsiella* sp., *Bacillus* sp., and *Pseudomonas* spp., have shown that they help to increase water permeability, nutrient uptake through roots, soil stability, soil fertility, plant biomass, chlorophyll content, root and shoot length, and surface area of leaves, while also helping to maintain metabolic and physiological activities during drought stress (Bhagat et al., 2021).

Gellan gum (Figure 2) and oligo-gellan coated on bulbs of *Eucomis bicolor* and *E. comosa* enhanced fresh weight of leaves and bulbs,

TABLE 1 Glycomolecules synthetized by different organisms such as bacteria, fungi, algae, and land plants. Abbreviations: AGP (arabinogalactan proteins); CPS (capsular polysaccharides); DGDG (digalactosyldiacylglycerols); EPS (exopolysaccharides); EXT (extensins); HRGP (hydroxyproline-rich glycoproteins); LPS (lipopolysaccharides); MEL (mannosyl-erythritol lipids); MGDG (monogalactosyldiacylglycerols); PGN (peptidoglycans); MLG (mixed-linkage glucans); PRP (Proline rich proteins); SQDG (sulfoquinovosyldiacylglycerides).

	Bacteria	Fungi	Algae	Land plants
Polysaccharides	EPS and CPS *(dextran, alternan, mutan, xanthan, gellan, wellan, rhamsan, glycogen, cellulose, alginate, fructans,…)*	α-D-Glucans *(amylose, glycogen, pullulan and mycodextran)* β-D-Glucans *(cellulose and β-D-glucopyranans)* Chitin and chitosan Polysaccharides with mannan main chain Polysaccharides galactan main chain	Storage polysaccharides *(laminaran, starch, inulin)* Cell wall polysaccharides *(cellulose, hemicelluloses and their analogs, alginates, ulvans, fucoidans, agar, carrageenans, pectins)*	Storage polysaccharides *(starch, fructans, galactans, galactomannans and glucomannans)* Cell wall polysaccharides *(cellulose, hemicelluloses, MLG, and pectins)*
Glycoproteins	PGN	Cell-wall *N*-glycans Cell-wall *O*-glycans Glycoprotein enzymes	Glycoproteins AGPs, EXTs Pherophorins	*N*-glycans *O*-glycans *(HRGP:AGPs, EXTs, and PRPs)*
Glycolipids	LPS Rhamnolipids, Rubiwettins, Trehalolipids, Other glycosylated mycolates, Oligosaccharide lipids, Glycosylated fatty alcohols, Glycosylated macro-lactones/−lactams, Glycocarotenoids/−terpenoids and Glycosylated hopanoids	MELs, Sophorolipids, Cellobiose lipids, Glucosyl-di-xylosyl lipids (Glykenins), Polyol fatty acid esters, Glucosyl and mannosyl lipids, Glycosylated polyketides, Glucosyl-galactosyl lipids, Glycosylated sterols and Glycosylated paraconic acids	MGDGs DGDGs SQDGs	MGDGs DGDGs SQDGs

chlorophyll content, net intensity photosynthesis, and macronutrient content in leaves (Salachna et al., 2018b). Drenching treatments with oligo-gellan on *Perilla frutescens* (L.) Britt. promoted plant growth, fresh weight of the aerial parts, antioxidant activity, and accumulation of nitrogen, potassium, magnesium, and phenolics. Such treatments also alleviated the negative effects of salt stress by limiting the loss of biomass, macronutrients, and phenolics by accumulating less sodium and having more photosynthetic pigments and antioxidant activity (Salachna, Grzeszczuk & Mizielińska, 2019). EPS are also known to be virulence factors for many plant pathogenic bacteria. Moreover, some plants can recognize EPS from specific bacteria, which can trigger the salicylic acid (SA) pathway and promote defense-gene expression and production of ROS (Milling et al., 2011). In addition, several purified components of EPS and CPS have a well-known elicitor activity. Indeed, β-D-glucans from bacterial cell walls elicited plant defense responses such as the induction of chitinase and phenylalanine ammonia-lyase (PAL) activities and the synthesis of isoflavanoids and phytoalexins (Chaliha et al., 2018). Bacterial fructans can be considered as microbe-associated molecular patterns (MAMPs) in plants due to their hydrolysis by fructan exohydrolases generating fructooligosaccharides (FOS), which can prime plant defenses (Versluys et al., 2017). Xanthan (Figure 2) is an important factor in bacterial pathogenicity and can elicit defense mechanisms in certain plant species by altering peroxidase activity (Luiz et al., 2016). Rhamsan has also been shown to induce the production of phytoalexins, including anthraquinones in *Morinda citrifolia* (Doernenburg and Knorr, 1994).

2.1.2 | Fungal polysaccharides

The main fungal polysaccharides are α-D-Glucans, β-D-Glucans, chitin, and chitosan (Figures 1 and 3; Gorin and Barreto-bergter, 1983). α-D-Glucan polysaccharides in fungi are amylose, glycogen, pullulan, and mycodextran (Figure 1). Amylose classically occurs in plants as storage polysaccharides and can also be found in several species from *Aspergillus*, *Bullera*, *Candida*, *Citeromyces*, *Cryptococcus*, *Fusicoccum*, *Penicillium*, *Rhodotorula*, *Tremella*, to *Trichosporon* genera (Gorin and Barreto-bergter, 1983). Glycogen classically occurs in animals and several fungi species from *Polyporus*, *Blastocladiella*, or *Trigonopsis* genera (Gorin and Barreto-bergter, 1983; Coté et al., 2008). Pullulan is a linear homopolysaccharide of D-glucopyranose residues, containing 1 → 4 and 1 → 6 glycosidic linkages, produced by many species of the fungus *Aureobasidium*. Mycodextran is synthesized by fungi from *Penicillium* and *Aspergillus* species. Its structure consists of alternating 3- and 4-linked α-D-glucopyranosyl repeating units. β-D-glucans in fungi are cellulose and β-D-glucopyranans (Figure 1). Cellulose, classically occurring in higher plant cell walls, is also the skeletal component of the cell walls of Acrasiales, Oomycetes, and Hyphochytridiomycetes. The cell wall taxonomy of fungi is based on fungal cellulose content in combination with other glycomolecules (cellulose-glycogen, cellulose-β-D-glucan, or cellulose-chitin). β-D-glucopyranans with 1 → 6 and 1 → 3 linkages are found in *Saccharomyces cervisiae* and *Candida* species. Branched-chain β-D-glucopyranans are produced by

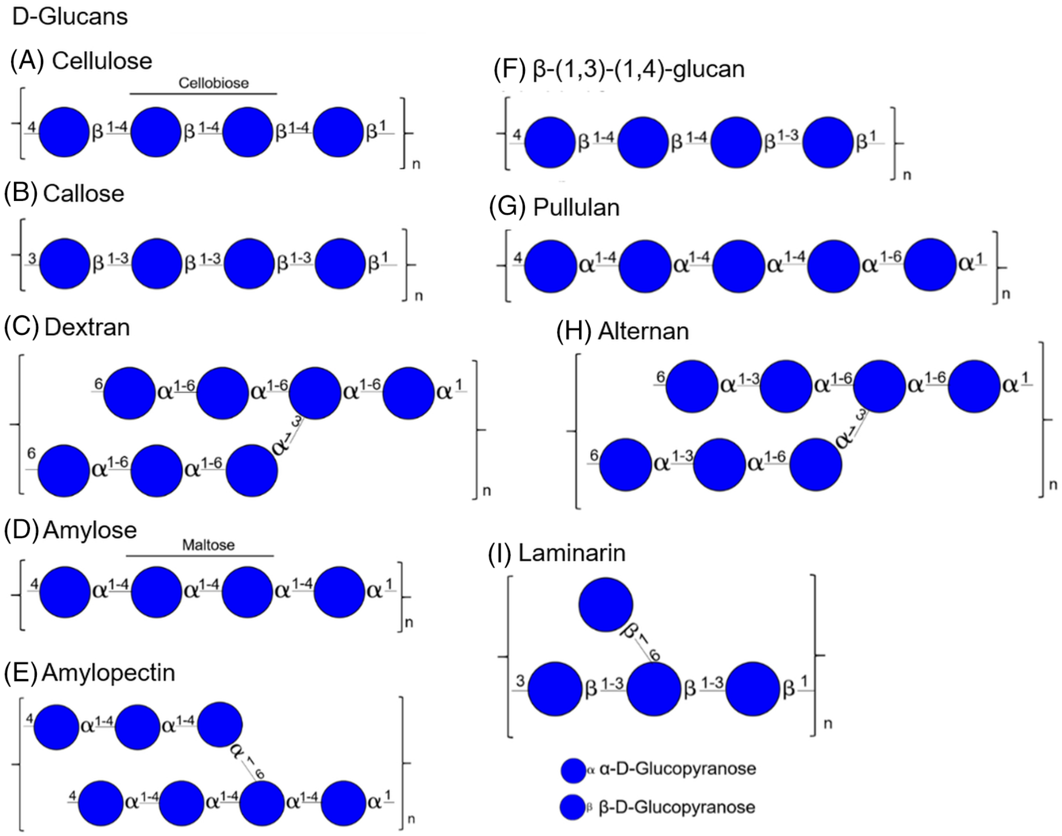


FIGURE 1 Several examples of β- and α-D-glucans. Cellulose found in the cell wall of algae, plants, and several bacterial genera (Lahiri et al., 2021), β-mix-glucans found in the cell walls of algae, fungi, and monocot plants from the Poales (Chang et al., 2021), callose found in the cell wall of plants particularly in pollen grains, pollen tubes and plasmodesmata (Li et al., 2023). β-(1–6), pullulan produced by strains of yeasts such as *Aureobasidium pullulans* (Singh et al., 2008), dextran found in the cell wall of *Lactobacillus hilgardii*, *Leuconostoc*, sp. and *Streptococcus* sp., alternan produced by the bacterium *Leuconostoc* sp. (Striegel et al., 2009), amylose and amylopectin found in plants and green algae floridean starch found in red algae, laminarin found in Stramenopiles including brown algae and diatoms (Chen et al., 2021). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

fungi such as *Aureobasidium pullulans*, *Sclerotium glucanicum*, or *Claviceps* sp. (Gorin and Barreto-bergter, 1983; Coté et al., 2008).

To the best of our knowledge, no studies have been devoted to fungal glucans as biostimulants. However, α-D-glucans from *Laetiporus sulphureus* have been found to stimulate wheat immunity by enhancing antioxidative activity, phenylpropanoids and lignin pathways, and pathogenesis-related (PR) protein synthesis (Nowak et al., 2022). Several other studies have shown the important role of fungal β-glucans in plant immunity (Chandrasekar et al., 2022; Fesel and Zuccaro, 2016).

Chitin is a linear polymer of β-(1 → 4)-linked 2-acetamido-2-deoxy-β-D-glucopyranosyl units found in many organisms such as filamentous fungi, yeasts, seaweeds, insects, worms, mollusks, and crustaceans (Figure 3). This analog of cellulose is found in several fungal genera like *Boletus*, *Cantharellus*, *Aspergillus*, *Armillaria*, *Psalliota*, *Candida*, and *Saccharomyces*. Chitosan, derived from chitin, is very similar to it, except that the *N*-acetyl-D-glucosamine is replaced by D-glucosamine, thus lacking *N*-acetyl groups (Figure 3). This polymer is present mainly in crustaceans and insects but can also be present in mycelia cell walls of certain fungi such as *Phycomyces* or *Mucor* genera (Coté et al., 2008).

Chitosan was initially reported as an elicitor of plant immunity by inducing ROS (hydrogen peroxide), PR proteins, nitric oxide (NO), and phytoalexin accumulation. Similarly, chitin induces hypersensitive responses, mitogen-activated protein kinase (MAPK) pathways, PR proteins (such as chitinase), and PAL activities (Chaliha et al., 2018). In addition, several studies have also reported that chitosan has biostimulant activities, including protection against abiotic stresses and enhancement of plant growth, yield, nutrient uptake, microorganisms associated with plant roots, and shelf life of flowers and fruits. These activities were found on a large panel of plants like vegetables, ornamental plants, and fruit crops, using several application forms, including seed coating, foliar spraying, culture substrate incorporation, or as a coating agent for post-harvest protection (Pichyangkura and Chadchawan, 2015; Shahrajabian et al., 2021). Other studies have also been performed on chitin as a biostimulant. The main forms of chitin application are foliar spraying, culture substrate application, and coating products to induce the same biostimulant activities as chitosan (Shahrajabian et al., 2021).

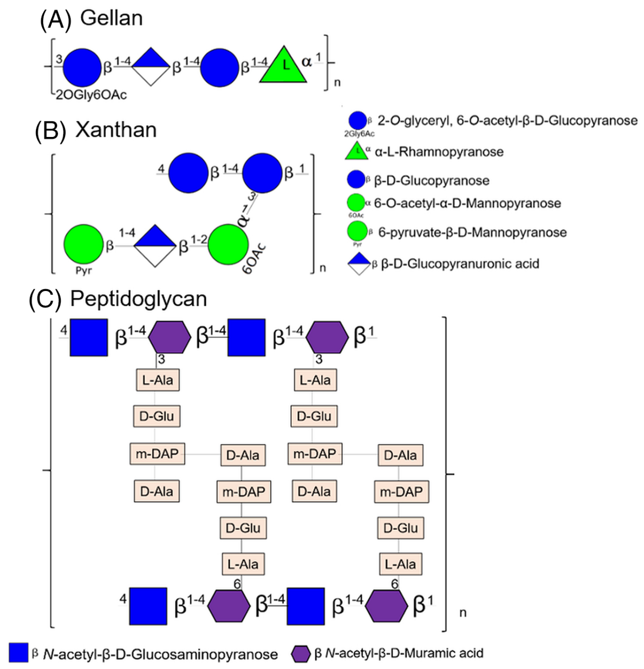


FIGURE 2 Structure of gellan and xanthan, exopolysaccharides produced by the bacteria *Sphingomonas* sp. (Sutherland 2007) and *Xanthomonas* sp. (Netrusov et al., 2023), respectively, and peptidoglycan found in the cell wall of gram-negative bacteria. The abbreviations shown correspond to: L-alanine (L-Ala), D-alanine (D-Ala), D-glutamic acid (D-Glu), and meso-diaminopimelic acid (m-DAP) (Vollmer et al., 2008). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

2.1.3 | Seaweed polysaccharides

Seaweed polysaccharides can be categorized as cell wall constituents or storage materials. Major storage polysaccharides are laminaran and starch (Figure 1). Major cell wall structural components are cellulose, hemicellulose, alginate, ulvan, fucoidan, agar, carrageenan, and pectin (Goñi et al., 2020). The occurrence of these algal polysaccharides is highly dependent on taxa. Indeed, red algae are characterized by floridean starch, glucomannan, sulfated mixed-linkage glucan, agar, carrageenan, and porphyran. Brown algae are characterized by laminaran, sulfated xylofucoglucan, xylofucoglucuronan, alginate, and fucoidan. Green algae are characterized by xyloglucan, mannan, glucuronan, and sulfated glucuronoxylorhamnan (ulvan) (Popper et al., 2011).

In storage polysaccharides, laminaran, also known as laminarin, is a glucan made up of glucose with β(1 → 3) linkages and β(1 → 6) or β(1 → 2) intrachain branching found in algae species such as *Ecklonia kurome*, *Laminaria japonica*, *Laminaria digitata*, and *Eisenia bicyclis* (Figure 1; Olatunji, 2020). Laminaran is very well known to elicit plant-defense responses such as phytoalexin, ROS, cytosolic Ca^{2+}influx, PR protein inductions, gene expressions of the SA signaling pathway, pattern-triggered immunity markers and transcription factors (Goñi et al., 2020; Wu et al., 2016; Mirande-Ney et al., 2023). It was also demonstrated to have biostimulant activities. Indeed, included in the culture substrate of *Arabidopsis thaliana* (L.) Heynh., laminaran promotes plant growth and tolerance to heat and salt stresses by regulating the defensin-like protein (DEFL) mediated pathways (Wu et al., 2016). A patent from Yvin et al., (1998) claims that this seaweed β-glucan improves seed germination of carrots (*Daucus carota* subsp. sativus (Hoffm.) Schübl. & G. Martens), lettuce (*Lactuca sativa* L.), and chicory (*Cichorium intybus* var. foliosum Hegi) when applied in the growth medium and enhances elongation of wheat coleoptiles (*Triticum aestivum* L.) after foliar spray. Carrasco-Gil et al., (2021) also showed that laminaran treatments enhanced seed germination and increased the root length of tomatoes (*Solanum lycopersicum* L.).

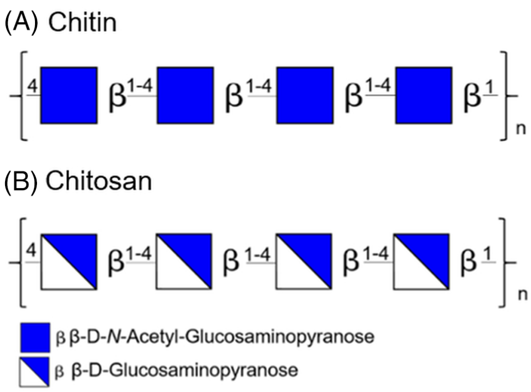


FIGURE 3 Structure of chitin found in the cell wall of fungi (Hou et al., 2021). Chitosan is a deacetylated form of chitin occurring naturally in Mucoraceae (Aranaz et al., 2021) or obtained chemically by alkali treatments. Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

Starch is the principal energy-storage carbohydrate of plants and an end product of photosynthesis. It is composed of two polymers: amylose and amylopectin (Figure 1). Amylose consists of a linear chain of α-(1 → 4)-D-glucose units, and amylopectin is also composed of α-(1 → 4)-D-glucose units but branched with α-(1 → 6) linkages. This major energy-storage carbohydrate occurs naturally in higher plants but is also present in red, brown, and green macroalgae and microalgae (Olatunji, 2020). Starch is also an essential substance in plant responses to abiotic stresses, such as water deficit and high salinity. Indeed, under challenging environmental conditions, aquatic and land plants generally remobilize starch to provide energy and carbon at times when photosynthesis becomes limited (Dong and Beckles, 2019). It is, therefore, used for many species as an acclimation strategy in harsh environments. Starch from algal origin has several applications, including in the textile, food, biomedical, pharmaceutical, and energy industries (Olatunji, 2020), but to date, no biostimulant or elicitor activities have been reported.

Alginate is the main polysaccharide found in the cell walls of brown seaweeds. It is a linear anionic polysaccharide, which consists of binary copolymers of the uronic acids β-D-mannuronic acid (M) and α-L-guluronic acid (G) units bound via β-(1 → 4) or α-(1 → 4) linkages (Figure 4).

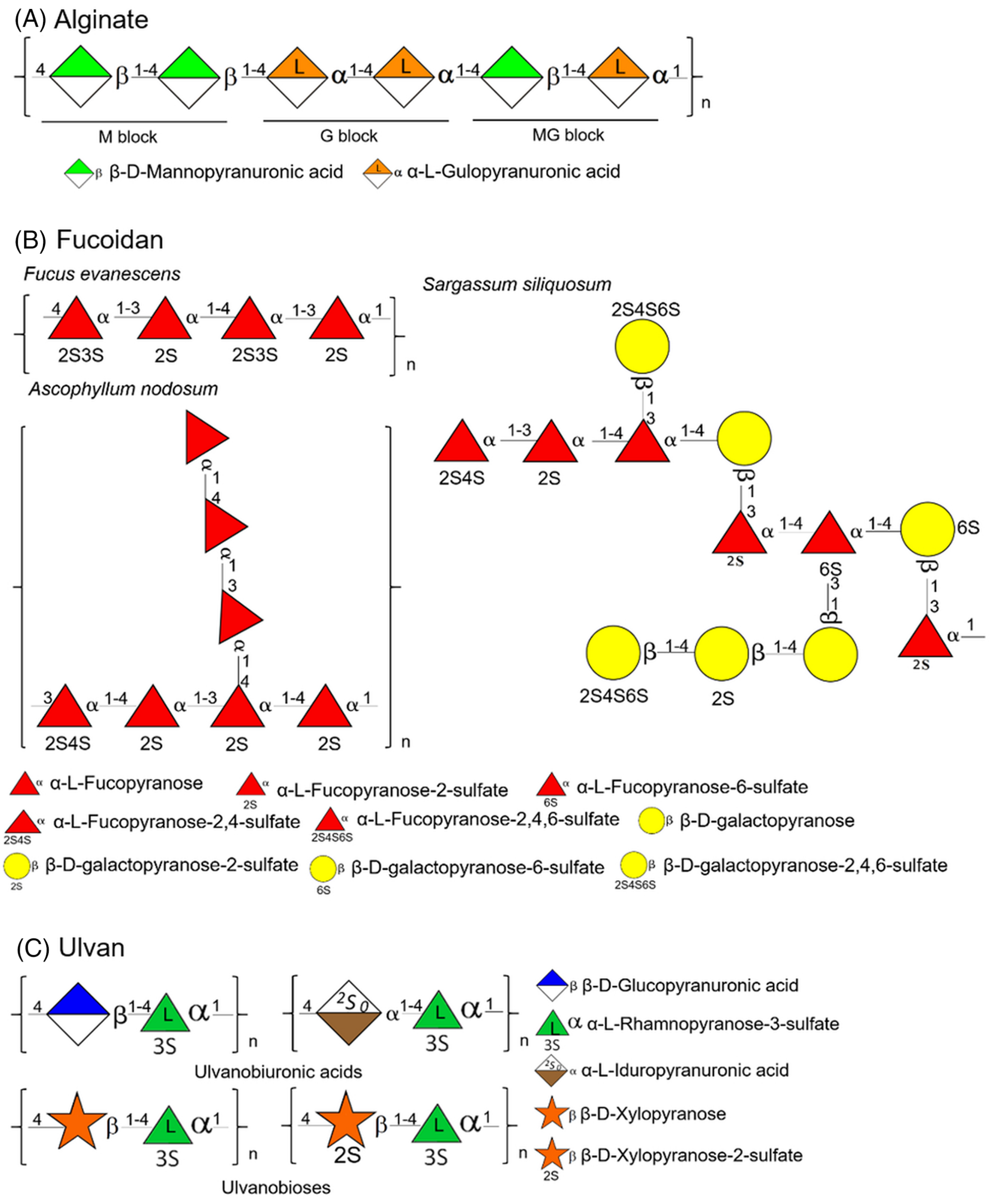


FIGURE 4 Structure of alginate and fucoidan found in the cell wall of Phaeophyceae and ulvan in the green algae *Ulva* sp. Alginates are found in *Laminaria* sp., *Macrocystis* sp., *Ascophyllum* sp., *Saccharina* sp., *Fucus* sp. *Sargassum* sp. (Guo et al., 2020). Fucoidans are sulfated fucose-rich polymers containing also, depending on the species: galactose, mannose, xylose, glucuronic acid, glucose and acetate groups. They are found in the cell wall of *Fucus* sp., *Ascophyllum* sp., *Sargassum* sp., *Macrocystis* sp., *Laminaria* sp., *Alaria* sp., and *Pelvetia* sp. (Li et al., 2008). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

Several studies have suggested that alginates and oligo-alginates induce resistance against plant pathogens such as viruses, bacteria, and fungi by blocking viral proteins, activate defense-related genes, e.g., PAL, superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), polyphenol oxidase (PPO), chitinase (CHI), and glucanase; or increase ROS, NO, flavonoids, and phytoalexin contents (Riseh et al., 2022). In addition, other studies have shown their biostimulant activities (Goñi et al., 2020). Indeed, foliar spraying of alginate oligosaccharides enhanced wheat (*T. aestivum*; Liu et al., 2013) and cucumber (*Cucumis sativus* L.; Li et al., 2018) tolerance to drought stress. Further, bulb coating limits the negative effects of salinity stress of umathunga (*Eucomis autumnalis* (Mill) Chitt; Salachna et al., 2018a). Moreover, seed coating was shown to enhance wheat tolerance to cadmium by increasing root and shoot lengths, fresh and dry weight, chlorophyll content, and antioxidant enzyme activities (SOD, CAT, and POD; Ma et al., 2010). Alginate-derived oligosaccharides with low molecular weights around 500–3000 Da and a higher ratio of mannuronate to guluronate (M/G ratios >1; indicating a lower viscosity) applied by coating on barley seeds (*Hordeum vulgare* L.) stimulated the growth of seedlings and roots, photosynthetic activity, and expression of development and stress tolerance-related genes like auxin response factor and MAPK (Yang et al., 2020). Some studies have shown that this oligoalginate, included in the culture medium, stimulated seed germination and increased the root length of lettuce (*L. sativa*) (Iwasaki and Matsubara, 2000) carrots (*D. carota* subsp. sativus), rice (*Oryza sativa* L.;Xu et al., 2003), maize (*Zea mays* L.; Hu et al., 2004), and tomatoes (*S. lycopersicum*; Carrasco-Gil et al., 2021).

Ulvans are sulfated heteropolysaccharides of green algae cell walls, especially in *Ulva* and *Enteromorpha* sp. They are composed of rhamnose (Rha; 17%–45%). Their structures consist of two main repeating disaccharides: the ulvabiuronic acid type A (β-D-GlcA (1 → 4) α-L-Rha 3S → 1) and type B (α-L-IdoA (1 → 4) α-L-Rha 3S → 1; Robic et al., 2008; Figure 4).

Several studies have used ulvan extracts as elicitors of plant immunity against various pathogens. Applied on several plants, they have been shown to enhance the expression of defense-related genes, the biosynthesis of phytoalexins, the amplification of oxidative bursts, and the activation of the jasmonic acid (JA) signaling pathway and antioxidant-related enzymes (Goñi et al., 2020). For biostimulant activities, ulvan-enriched extracts obtained from *Ulva lactuca* promoted seed germination and stimulated growth and rooting of tomato (*S. lycopersicum*) and mung bean plants (*Vigna radiata* (L.) R. Wilczek; Hernández-Herrera et al., 2016). Moreover, ulvans applied by foliar spraying or included in the growth or culture medium induced genes involved in nitrogen absorption of *Medicago truncatula* Gaertn., a significant effect on mineral nitrogen absorption in wheat (*T. aestivum*), and increased protein content in peas (*P. sativum*) and maize (*Z. mays*; Briand et al., 2011). In terms of abiotic stress tolerance, ulvans applied to the leaves or roots of maize enhanced the plant biomass under heat and drought stresses (Goñi et al., 2020). More recently, Shefer et al., (2022) showed that ulvans extracted from cultivated green algae *Ulva* sp. and added to the growth medium stimulated length and weight of roots, shoots, and total plants of *A. thaliana*.

Fucoidans or algal fucans are composed of sulfated α-L-fucose backbones with small amounts of other monosaccharides, including D-glucose, D-galactose, D-mannose, D-xylose, D-glucuronic acid, and acetyl groups (Figure 4).

Fucoidans have been identified with a range of bioactive properties, which give them potential applicability in the food, cosmetics, pharmaceutical, and biomedical industries (Olatunji, 2020). In agricultural applications, several studies have investigated the elicitation of plant defense against phytopathogens (Goñi et al., 2020). These studies reported the release of H_2O, stimulation of PAL, lipoxygenase (LOX), and glutathione S-transferase (GST) enzymes, and the accumulation of SA, phytoalexins, and PR proteins (Goñi et al., 2020). However, only one study reported a biostimulant activity of fucoidans from *Macrocystis pyrifera*, which were shown to induce plant resistance to salt stress in wheat when applied by foliar spray (*T. aestivum*; Zou et al., 2021).

Carrageenans, sulfated galactans, are linear polysaccharides composed of repeating dimers of D-galactose, which are linked via alternated bonds of α-1,3 and β-1,4 and substituted by one (κ-carrageenan), two (ι-carrageenan), or three (λ-carrageenan) sulfate ester groups within each repeating unit (Figure 5).

Carrageenans and oligo-carrageenans facilitate plant growth through several metabolic processes, including chlorophyll metabolism, carbon fixation, photosynthesis, protein synthesis, secondary metabolite generation, and detoxification of ROS. In parallel, these compounds suppress pathogens by their direct antimicrobial activities and improve plant resilience against pathogens by modulating biochemical changes via SA and JA and ethylene (ET) signaling pathways, resulting in increased production of secondary metabolites, defense-related proteins, and antioxidants.

Carrageenans are known to induce plant-defense responses against viruses, viroids, bacteria, fungi, and insects by stimulating JA, SA, and ET signaling pathways (Goñi et al., 2020; Mukarram et al., 2021). However, when (κ, ι, or λ)-carrageenans were applied via seed coating and foliar spraying, several other studies have demonstrated biostimulant activities on quality traits of various plants, including *V. radiata*, *Foeniculum vulgare* Mill., *Cicer arietinum* L., *Z. mays*, *Eucalyptus globulus* Labill., *Arachis hypogaea* L., *Nicotiana tabacum* L., *Ocimum basilicum* L. The application of these carrageenans also enhanced nutrient efficiency in *Pinus radiata* D. Don and enhanced drought stress tolerance in *Cymbopogon flexuosus* Steud (Goñi et al., 2020; Hossain et al., 2024; Mukarram et al., 2021).

Agar is a mixture of two polymers, agarose and agaropectin. Agarose is a neutral linear polymer consisting of 3-O substitute β-D-galactopyranosyl and 3,6-anhydro-α-L-galactopyranosyl repeating units, while agaropectin is charged with sulfate groups (Figure 5). Agar is a well-established biopolymer obtained from red algae, mainly from *Gracilaria* sp. and *Gelidium* sp., which has diverse applications in the food, biotechnology, cosmetics, and pharmaceutical industries (Olatunji, 2020). There is still a lack of studies regarding agricultural utilization of agar. To the best of our knowledge, no study has dealt with plant-defense responses on land plants. Only a few studies on macroalgae have shown the plant-defense activities of agar and oligo-agar. Oligo-agar applied in seawater medium elicited a response in the red alga *Pyropia haitanensis* T.J. Chang & B.F. Zheng by reducing the rotting rate of the algae, enhancing oxidative bursts, increasing volatile organic compounds, phospholipase A2 activity, and decreasing free fatty acid contents (Wang et al., 2013). *Gracilaria* sp. also responded by enhancing oxidative bursts with hydrogen peroxide when oligo-agars were added to the medium (Weinberger et al., 2005, 2010).

As for biostimulant activities, a study showed that agar extracted from the red seaweed *G. gracilis* applied in the culture medium improved the growth and seed germination of *Brassica oleracea* L. (Pacheco et al., 2021). Another study indicated that agar promoted the growth of *Amaranthus viridis* L. when applied to soil under drought stress conditions (Mahusook et al., 2021). This observation aligns with the recent review on natural superabsorbent glycopolymers, such as agarose, cellulose, starch, and alginate, as water-saving products and soil conditioners in agriculture because of their water-retention properties (Behera and Mahanwar, 2019).

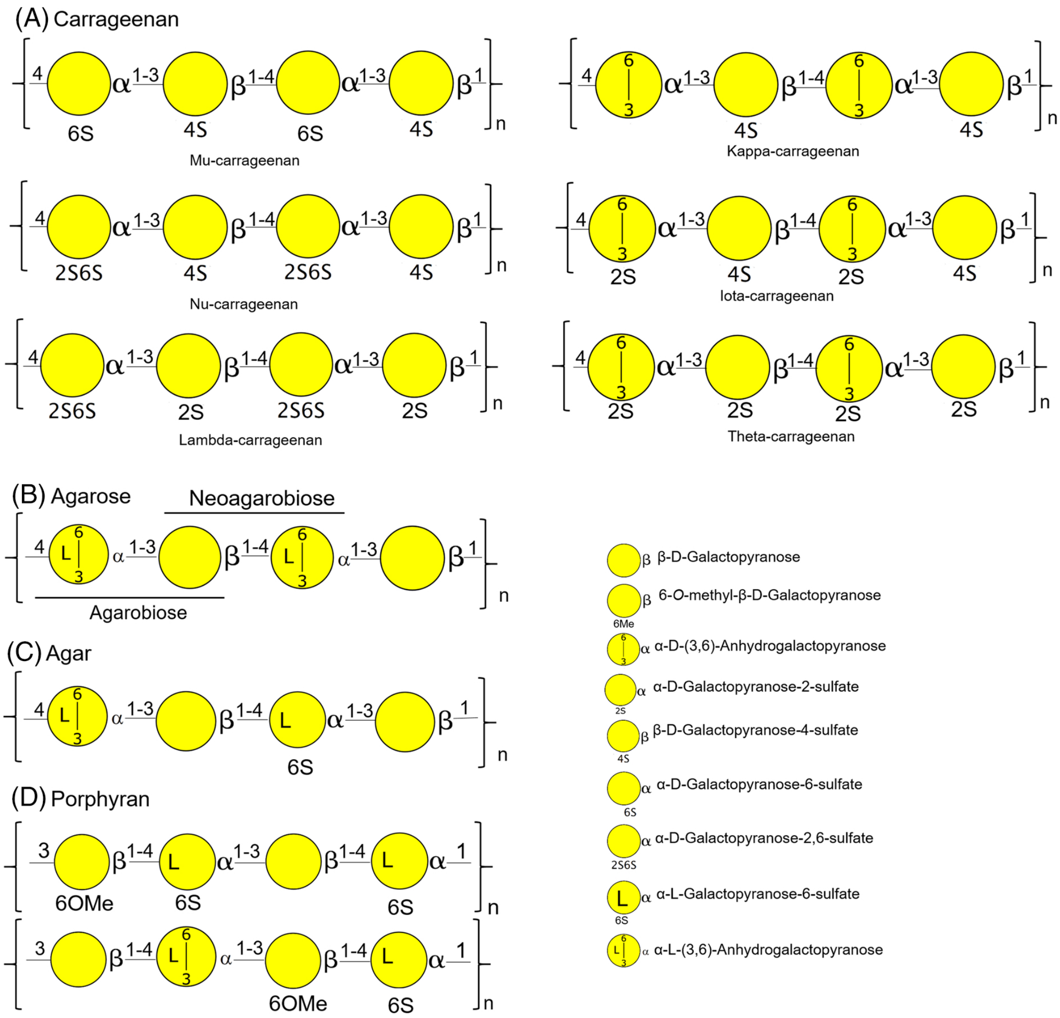


FIGURE 5 Structure of galactans and sulfated galactans found in the cell wall of Rhodophyta. Carrageenans are found in the cell wall of *Kappaphycus* sp. which is the main source of industrial kappa-carrageenan, *Euchema* sp. as the the main source of industrial iota-carrageenan, *Gigartina* sp. as the main source of industrial lambda-carrageenan and *Chondrus* sp. Agarose and agar are found in the cell wall of *Gelidium* sp., *Gracilaria* sp., *Pterocladiella* sp., *Ahnfeltia* sp., *Pyropia* sp. Porphyrans are found in the cell wall of *Porphyra* sp. (Ciancia et al., 2020). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

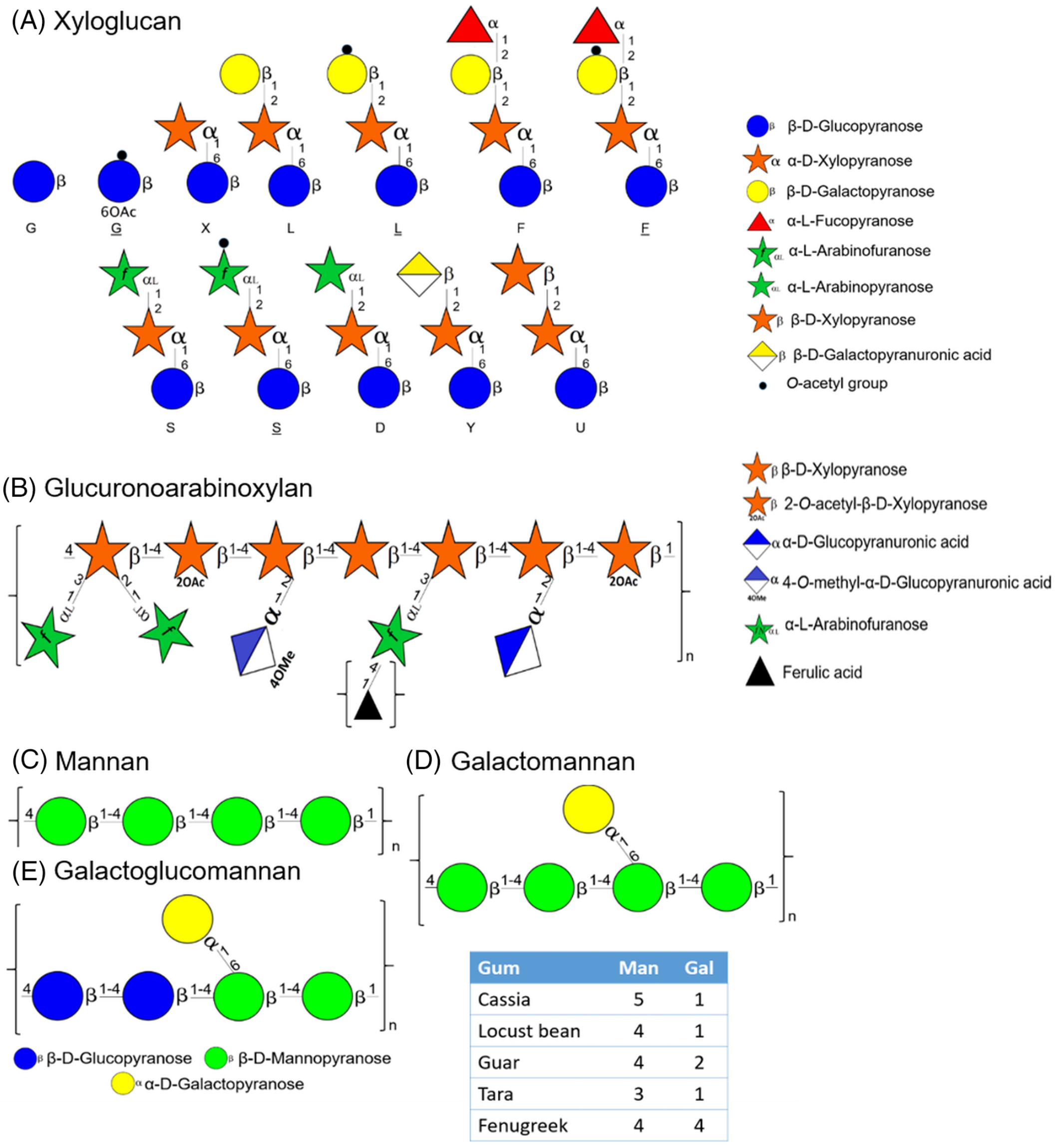
Porphyran and oligo-porphyran (Figure 5) have a wide range of applications in medicine, cosmetics, and food due to their antioxidant, immune-modulating, anti-aging, and antimicrobial activities (Wang et al., 2023). But to date, no agricultural application has been reported.

Cellulose, pectins, and hemicelluloses are polysaccharides shared with land plants. Algae sources of cellulose include red, brown, and green macroalgae. Cellulose is a linear polymer made up of chains of β-(1 → 4)-linked glucose residues (Olatunji, 2020; Figure 1). Hemicelluloses and their analogs also are found in the cell walls of green, red, and brown seaweeds (Figure 6). Pectin is typically found in land-plant cell walls (Figure 7). But some forms of pectins are also found in macroalgae and marine diatoms (Arnosti et al., 2021; Vidal-Melgosa et al., 2021).

Cellulose, pectins, and hemicelluloses from algae seemed to have no research reports available on their agricultural applications even though they are widely studied for bioethanol production, preparation of paper, nano and microcrystalline polymers, or bioplastics (Baghel et al., 2021).

2.1.4 | Microalgae

Compared to macroalgae, the applications of microalgae extracts in agriculture are still very limited, and much less is known regarding their biostimulant activities even if different microalgae-based products are commercially available to improve plant yields (Ronga et al., 2019). Microalgae have a wide range of applications mostly in nutraceutical, pharmaceutical, and cosmetic industries. However, there are some opportunities to exploit microalgae as plant biostimulants especially regarding the worldwide demand of the circular economy and valorization of coproducts from these precited industries. Moreover, there is a growing interest to use microalgae for the



Gum	Man	Gal
Cassia	5	1
Locust bean	4	1
Guar	4	2
Tara	3	1
Fenugreek	4	4

FIGURE 6 Structure of hemicelluloses. Several examples of the diversity of side chains found in xyloglucan depending on the species, organ and tissues (Schultink et al., 2014; Dehors et al., 2019) using the one letter code proposed by Fry et al., (1993). Xylan-type hemicellulose has been described as unbranched xylan backbone, arabinoxylan (AX), glucuronoarabinoxylan (GAX), and 4-O-methyl-GAX (Scheller and Ulvskov, 2010). Ferulic acid is only found in the cell walls of commelinid monocots. Mannan-type hemicellulose can be found as mannan, galactomannan and galactoglucomannan (Scheller and Ulvskov, 2010). Galactomannan gums such as cassia are found in *Cassia* sp. and *Senna* sp., locust in *Ceratonia siliqua*, guar in *Cyamopsis* sp., tara in *Caesalpinia spinosa* and fenugreek in *Trigonella foenum-graecum* seeds (Dhull et al., 2022). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

development of biostimulants as demonstrated by very recent published papers (Braun and Colla, 2022; Prisa and Spagnuolo, 2023; Renaud et al., 2023; Santoro et al., 2023). A recent review also explored these polysaccharides as promising plant biostimulants in showing effects on plant growth, nutrient uptake, and tolerance to abiotic stress (Chanda et al., 2019). This promising use is based on (1) microalgae polysaccharide composition, which is close to that of macroalgae; (2) recent studies on their applications as plant biostimulants; and (3) their ability to function as defense elicitors (D/MAMPs).

1. For microalgae polysaccharide composition, in contrast to macroalgae for which the major cellular components are carbohydrates, the major components of microalgae are usually proteins and lipids (Gao et al., 2020). However, in terms of structure, several microalgae species exhibit polysaccharides, glycoproteins, and glycolipids close to those of macroalgae with valuable bioactive medical properties such as antioxidant, anti-microbial, or anti-tumor capacities (Martínez-Francés and Escudero-Oñate, 2018).
2. For their applications as plant biostimulants, polysaccharide extracts of *Dunaliella salina* and *Porphorydium* sp. (containing respectively

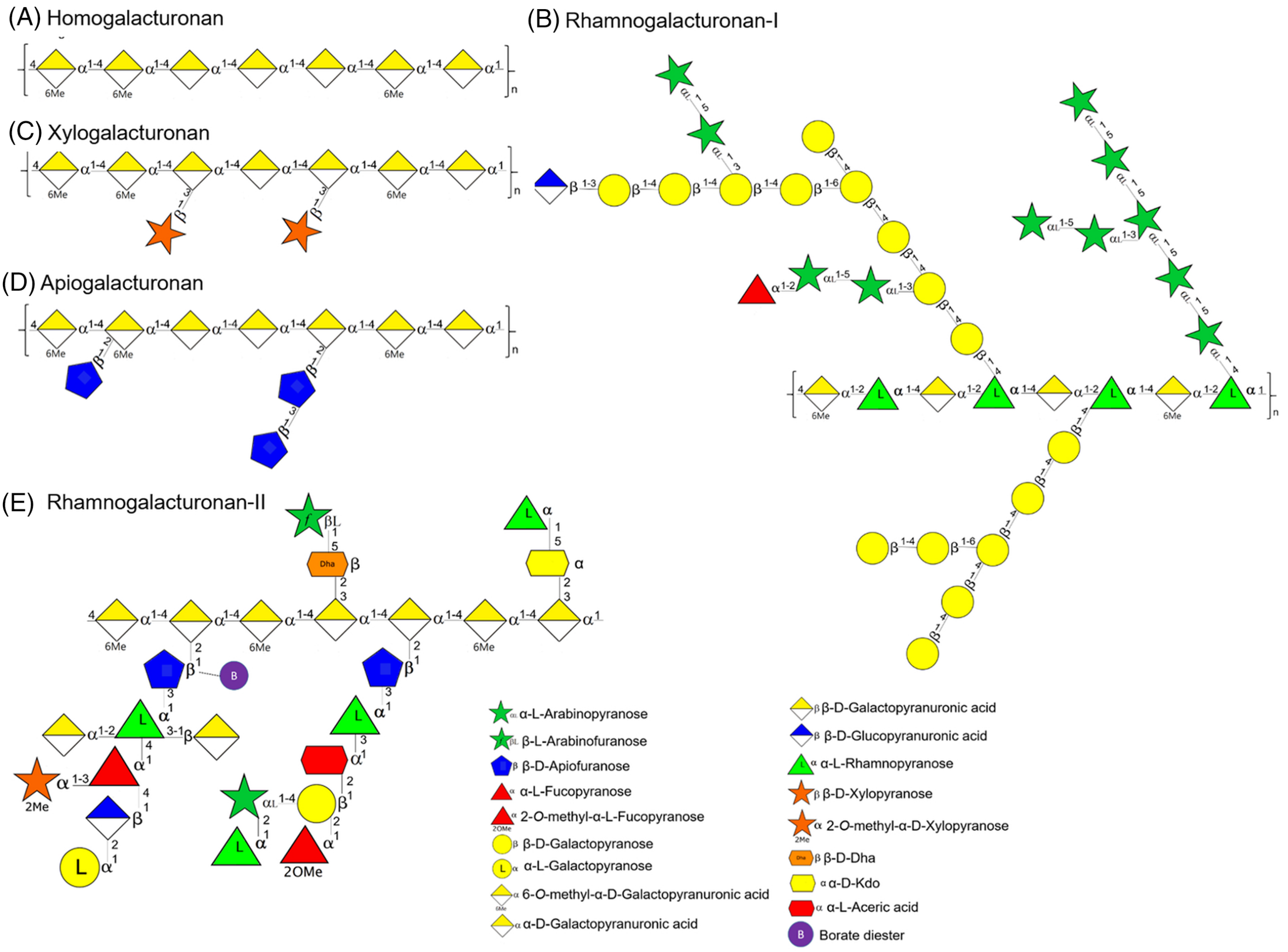


FIGURE 7 Structure of the five pectin domains found in the cell wall throughout land plant lineages (Wolf et al., 2012). Homogalacturonan can be found with various degrees of methylesterification from high to weak. Xylogalacturonan can be found in low amounts in the cell walls of many organs and tissues (Zandleven et al., 2007). Apiogalacturonan is mostly found in the cell walls of aquatic monocot plants (Lemnoidae) and bryophytes (Matsunaga et al., 2004; Avci et al., 2017). Rhamnogalacturonan-I (RG-I) is the second most abundant pectin motif. Rhamnosyl residues are branched with various sizes of galactan, arabinan, and arabinogalactan side chains (for more details, see Kaczmarska et al., 2022). Rhamnogalacturonan-II (RG-II) is a highly complex and conserved motif with unusual carbohydrates such as apiose, Kdo, aceric acid and Dha. Slight structural changes in structure occur depending on the species. For more details see Lerouge et al., (2021). Abbreviations: Dha, 3-Deoxy-D-lyxo-hept-2-ulopyranosaric acid; Kdo, 3-Deoxy-D-manno-oct-2-ulopyranosonic acid. Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

33% and 35.3% of neutral sugars, 23.9% and 13.8% of uronic acids, and 11.5% and 10.4% of sulfate groups) were applied in a culture medium of *S. lycopersicum*. They caused an increase in number of nodes, shoot dry weight, shoot length, carotenoid, chlorophyll, and protein contents and nitrate reductase and NAD-glutamate dehydrogenase activities in leaves. The authors hypothesized that growth stimulation was mainly correlated to sugar content and sulfated and carboxylated groups (uronic acid) of polysaccharides (Rachidi et al., 2020).

Polysaccharide extracts of *Chlorella vulgaris* coated on seeds of wheat (*Triticum vulgare* L.) and French beans (*Phaseolus vulgaris* L.) increased their growth parameters, including dry and fresh weights, leaf area, shoot height, and root length, photosynthetic pigment carbohydrate and protein contents, and antioxidant activities in seedling leaves. The polysaccharide extract used contained six monosaccharide and disaccharide units, fructose, glucose, maltose, lactose, rhamnose, and arabinose in addition to other components like sulphate, uronic acids, and proteins (El-Naggar et al., 2020).

Exopolysaccharide extracts of *Dunaliella salina*, containing 46.9% neutral sugars, 8.3% uronic acids, and 2.8% sulfate groups, applied on *S. lycopersicum* by foliar spraying increased plant growth, balanced K^+/Na^+ ratios, and induced very long-chain fatty acid (VLCFA) biosynthesis involved in the wax construction in salt stress conditions (El Arroussi et al., 2018).

Paramylon, a β-1,3-glucan purified from euglenoids, added to the nutrient solution of *S. lycopersicum* grown in an aeroponic system increased plant resistance to drought stress and improved content of the fruits in their antioxidant compounds (carotenoids, phenolic acid, and vitamins) and soluble carbohydrate content e.g. glucose, fructose, and sucrose (Barsanti et al., 2019).

3. Regarding their ability to function as defense elicitors, microalgae polysaccharides seem to be recognized as D/MAMPs as do certain macroalgal polysaccharides. Indeed, sulfated exopolysaccharides derived from *D. salina* enhanced the accumulation of proline, ROS, and enzyme activities (CAT, POD, SOD) in tomatoes under saline stress (El Arroussi et al., 2018). Moreover, PAL, chitinase, β-(1,3)-glucanase, and peroxidase (POX) activities were increased in tomato leaves treated with polysaccharides extracted from *Desmodesmus* sp., *Phaeodactylum tricornutum*, *Porphyridium* sp., and *D. salina*. They also induced the accumulation of proteins, polyphenols, H_2O_2, fatty acids, alkanes, alkenes, phytosterols, and azelaic acid, most of which are signaling and regulator molecules of plant defense (Rachidi et al., 2021). *Chlorella vulgaris*, *Chlorella sorokiniana*, and *Chlamydomonas reinhardtii* polysaccharides stimulated enzymatic activities of ascorbate peroxidase (APX) and POD in tomato plants (Chanda et al., 2019).

2.1.5 | Land-plant polysaccharides

As seaweeds and marine grasses, land plants have polysaccharides for energy-storage and cell-wall composition. Major energy-storage glycomolecules are starch, fructan, galactan, galactomannan, and glucomannan. Starch (Figure 1) is a major energy-storage carbohydrate implicated in plant stress mitigation by remobilising its reserves to release energy, sugars and derived metabolites.(Dong et al. 2019; see also Section 1.1.3). However, no study has reported the use of land-plant starch as a biostimulant. Though, some agricultural applications have explored its use as a pesticide or a fertilizer-delivery system and as a natural superabsorbent glycopolymer to preserve soil moisture (Das et al. 2020). Similarly, very few studies have mentioned its elicitor activities. Soluble starch from potatoes applied in culture growths of different *Hypericum* species showed an increase of several phenolics like kaempferol-3-O-glucoside, chlorogenic acid, catechin, rutin, amentoflavone, and phloroglucinol (Bálintová et al., 2019).

Three types of fructans exist: inulin, graminan, and levan (Figure 8), comprised of β-D-fructose units. Levan is also an exopolysaccharide produced by bacteria (see Section 2.1.1). Different types of fructans are found in plants depending on the linkage type and branching (Figure 8), including inulins (β-2,1-fructosyl bonds), levans (β-2,6-fructosyl bonds), graminans (mix of β-2,1 and β-2,6-fructosyl bonds), and neokestose-type inulins and levans as well as complex, mixed-type fructans (agavin; Versluys et al., 2017). Fructans have either β-2,1 (inulin), β-2,6 (levan), or a mix of both (graminan) glycosidic bonds (Figure 8). Dicot plants mainly produce inulin while levan, mixed-type fructans (graminans) and neokestose-based fructans are mostly found in monocots (Versluys et al., 2017). Aside from their energy-storage functions, they are associated with stress-tolerance mechanisms, such as freezing and drought stress, and as osmoprotectants. However, despite this osmoprotective activity, we have not found any report on the use of these compounds as biostimulants (Jiménez-Arias et al., 2021). Several studies have highlighted their action as elicitors of plant defense against phytopathogens (Versluys et al., 2017). Indeed, inulin, levan, or fructooligosaccharides improved plant resistance to infection in *A. thaliana*, *L. sativa*, *S. lycopersicum*, *Vitis labrusca* L., *Malus domestica* Borkh., and *C. sativus* (Versluys et al., 2017; Janse van Rensburg et al., 2020).

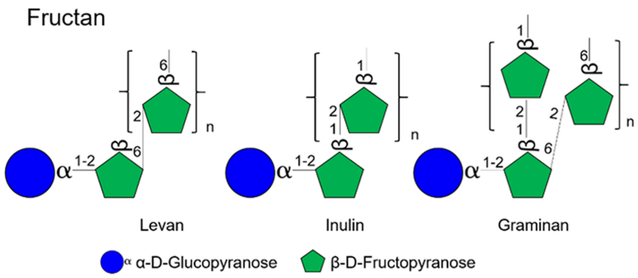


FIGURE 8 Structures of fructans found in plants. Levan, inulin and graminan are storage polymers (Wang et al., 2023). Fructans are also present in bacteria (see Section 1.1.1) and fungi (see Section 1.1.3) (Netrusov et al., 2023). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

Fructans are also present in bacteria (see Section 1.1.1) and fungi (see Section 1.1.3). Interestingly, Versluys et al., (2017), Versluys and Van 2022) have proposed a potential role of microbial fructans as MAMP and plant fructans as DAMP giving them a priming status to future biotic and abiotic stress management. Inulin from chicory roots can trigger Arabidopsis resistance against *Botrytis cinerea* by increasing H_2O_2, ROS-scavenging enzymes, NADPH-oxidase, and sugar content (Janse van Rensburg et al., 2020).

Other energy-storage polysaccharides include cell-wall polysaccharides such as pectins and hemicelluloses e.g. galactomanan and glucomannan.

The cell wall plays a role in the growth, differentiation, mechanical integrity, and interface between cells and the environment (Somerville, 2004). Cell-wall polysaccharides are cellulose, hemicelluloses, and pectins. Hemicellulose and pectins are assembled in the Golgi apparatus and then transported via Golgi-derived vesicles to the cell wall. By contrast, cellulose is synthesized at the plasma membrane. Together, hemicelluloses and pectins constitute the matrix in which cellulose microfibrils are embedded. In both primary and secondary cell walls, cellulose, hemicelluloses, and pectins are mixed, and the interactions among the different polysaccharides ensure both strength and flexibility of the cell wall (Somerville, 2004).

Cellulose is the most abundant cell wall component among the polysaccharides with 30–70% of the cell wall composition. It occurs in all higher plants and some algae, fungi, bacteria, and certain animals like truncates and protozoans. It is a linear homopolysaccharide (Figure 1; see also Section 2.1.3) forming six long and rigid microfibrils, organized in six macrofibrils, synthesized by cellulose synthase complexes and delivered to the plasma membrane (Anderson and Kieber, 2020).

Cellulose from land plants has numerous applications in various industrial fields such as the manufacturing of paper and cardboard, textiles, pharmaceuticals, biofuels, and food (Gupta et al., 2019). Recent studies on agricultural applications have explored cellulose's potential in holding water and water-soluble fertilizers in the soil (Das et al., 2020; França et al., 2021).

To the best of our knowledge, very few studies have been carried out on the biostimulant activities of cellulose. The application of this polysaccharide in the soil of *O. sativa* influenced rhizosphere enzymatic activities under phosphorus fertilization (Wei et al., 2019). Cellobiose, a dimer of cellulose (Figure 1), was shown to increase fresh weight of *A. thaliana* seedlings when applied in high concentrations in the culture medium (Souza et al., 2017). Moreover, oligomers of cellulose have been reported as DAMPs in plant immunity. Aziz et al., (2007) were able to induce defense responses in *Vitis vinifera* L. including oxidative bursts, elevation of free cytosolic Ca^{2+}, and the expression of PR genes. Souza et al., (2017) also showed that cellobiose applied to Arabidopsis seedlings induced overexpression of WRKY transcription factor genes, triggered early Ca^{2+} transient, and activated MAPKs signaling cascade and suberin biosynthesis.

Hemicellulose, ca. 20–40% of the cell wall, and cellulose are structurally related compounds (see also Section 2.1.3) and are closely associated in the cell wall. Both of these heteropolysaccharides are characterized by a backbone of β-1,4-linked sugars and are grouped into three classes: (1) glucans like xyloglucan and β-glucan, (2) xylans like xylan and arabinoxylan, and (3) mannans like glucomannan and galactoglucomannan (Scheller and Ulvskov, 2010). Xyloglucans are the most abundant hemicelluloses in the primary cell walls of eudicots. They are heteropolysaccharides composed of backbones of β-1,4-linked glucan with side chains of xylose, galactose, fucose, or arabinose residues and others (Figure 6; Fry, 2010). Oligoxyloglucans (XGOs) derived from the breakdown of xyloglucan in plant cell walls are emerging as biostimulants. Indeed, a study has shown that XGOs included in culture media stimulated growth of *A. thaliana* (González-Pérez et al., 2012). The XGOs implicated in this biostimulant activity are mainly XLLG and XXLG and in lower proportions XXXG and XXGG according to xyloglucan nomenclature (Fry et al., 1993). XGOs in the culture medium also increased salt stress tolerance of Arabidopsis by enhancing CAT gene expression, POX activity, and chlorophyll a/b ratios while reducing protein oxidation and total polyphenol content (González-Pérez et al., 2018). These XGOs had the same effect on *N. tabacum* seedlings under salt stress conditions by increasing the number of leaves, primary root length, lateral root formation, and proline and chlorophyll contents and reducing protein oxidation and lipid peroxidation (Páez-Watson et al., 2020). In addition, a patent claims that foliar application of XGOs improves cold stress resistance in *V. vinifera* and *Actinidia deliciosa* (A. Chev.) C.F. Liang & A.R. Ferguson (Salvador and Lasserre, 2010).

Xyloglucan oligosaccharides are also considered DAMPs. They elicited MAPK activation and immune gene expression like PR, phytoalexin deficient (PAD), and defensins in *V. vinifera* and *A. thaliana* (Claverie et al., 2018). Additionally, the authors demonstrated that xyloglucan conferred resistance against the pathogens *Botrytis cinerea* and *Hyaloperonospora arabidopsidis*.

Xylans are the predominant hemicelluloses in the cell walls of monocot plants. These polysaccharides have a xylose-containing backbone that is decorated with 4-*O*-methyl-D-glucopyranuronic acid, D-glucopyranuronic acid, L-arabinofuranosyl, and/or L-arabinopyranosyl units (Figure 6; Coté et al., 2008). Xylooligosaccharides (XOS), produced from xylan by enzymatic hydrolysis, applied in the culture substrat of *Brassica rapa* L. improved growth and tolerance to salinity stress by enhancing antioxidative systems, both enzymatic and non-enzymatic antioxidants, reduced lipid peroxidation, and increased the accumulation of osmolytes and the maintenance of the ionic balance (Chen et al., 2015). Applied to the soil of *S. lycopersicum*, XOS promoted the flowering of the plant, soil bacterial and actinomycete population, soil microbial biomass, nitrogen and phosphate content, and soil urease and phosphatase activities (Chen et al., 2012). Furthermore, XOS demonstrated plant defence properties, which were evidenced by the elicitation of stomatal closure via the salicylic acid (SA) signalling-mediated production of reactive oxygen species (ROS) and nitric oxide (NO, Zhang et al., 2021).

Arabinoxylan-oligosaccharides and mixed-linked glucans also act as DAMPs in triggering immune responses including Ca^{2+} influx, ROS production, MAPK phosphorylation, expression of pattern-triggered immunity (PTI)-related genes, and enhanced pathogen resistance (Mélida et al., 2020; Rebaque et al., 2021).

Mannans, homopolymers of (1 → 4)-linked β-D-mannosyl residues, occur as storage polysaccharides and as structural polysaccharides in the primary and secondary cell walls of plants (Figure 6; Melton et al., 2009). Galactomannans are heteropolysaccharides with a main β-(1 → 4) mannose chain to which α-D-galactose units in *O*-6 positions are attached. They are closely related to plant gums and are found in soft-wood trees and seeds of several Fabaceae. Glucomannans are also heteropolysaccharides consisting of β-(1 → 4)-glucose and mannose units to form a linear polymer occasionally branched with galactose (galactoglucomannans).

Galactomannans are used in several industries such as cosmetics, food, drilling, explosives, paper, petroleum, pharmaceuticals, and textiles (Lavudi and Suthari, 2020). Due to their water-soluble, stable, and highly viscous properties, they are also used in agriculture as water-retaining and/or pesticide- and fertilizer-delivery agents. Glucomannans also have food, biomedical, chemical, and environmental applications as absorbents for removal of pollutants (Yang et al., 2017).

We found no study on biostimulant activities of galactomannans or glucomannans. However, Zang et al., (2019) showed that oligomannans from Locust gum, applied to leaves of *Nicotiana benthamiana* Domin. and *Oryza sativa*, triggered various defense and resistance responses including elevation of intracellular Ca^{2+}, ROS bursts, activation of MAPK and defense-related genes, hypersensitive cell death, and stomatal closure.

Pectins are the most complex polysaccharides in nature and the most abundant in the primary cell wall. Their structure mainly consists of galacturonic acid in the main chain and neutral sugars in the side chains. The main pectin domains are homogalacturonan (HG), rhamnogalacturonan-I (RG-I), rhamnogalacturonan II (RG-II), and xylogalacturonanes (Figure 7). Some other pectin motifs exist but are minor or plant-specific such as xylogalacturonan and apiogalacturonan. HG consists of 1,4-linked α-D-galacturonic acid and RG-I has a backbone of 1,4-α-D-Gal*p*A-1,2-α-L-Rha*p* disaccharide repeating units with side chain decorations on the rhamosyl residues e.g. arabinan, galactan, or arabinogalactan. RG-II is a highly complex molecule with a backbone of 1,4-linked α-D-Gal*p*A units to which four to six structurally conserved side chains are attached, consisting of twelve different monosaccharides like GalA and unusual sugars such as apiose, aceric acid, Kdo, and Dha (Lerouge et al., 2021; Yapo et al., 2007). Even though pectins are mainly found in land-plant cell walls, some forms are also found in seagrasses. Indeed, pectin isolated from the marine seagrass *Zostera marina* or the freshwater duckweed *Lemna minor* consists predominantly of apiogalacturonan. Apiogalacturonan is an HG backbone decorated with relatively frequent substitutions at *O*-3 of single residues or short oligosaccharides of D-apiose (Avci et al., 2017; Khasina et al., 2004). RG-I branching, as well as methyl- and acetylesterifications, has also been detected in the marine seagrass.

Several studies have highlighted pectin and their oligomers as biostimulants. Indeed, a study demonstrated that pectin-rich amendments can enhance *Bacillus velezensis*-mediated soybean growth promotion and nodulation by indigenous and inoculated *Bradyrhizobium japonicum* (Hassan et al., 2019). The application of aqueous solutions of citrus peel pectin nanospheres by dipping wheat seeds resulted in enhanced germination, the seeding stage, and net photosynthetic rate, as well as increased nutrient uptake (Li et al., 2021). Pectin-derived oligosaccharides with a degree of polymerization (DP) from three to six, applied on berries of *V. vinifera*, enhanced the synthesis and accumulation of anthocyanins and change of expression of key genes of the phenylpropanoid pathways (Villegas et al., 2016). Oligogalacturonides applied on tomato fruits promoted ripening by inducing ethylene (ET) synthesis through the regulation of ET synthesis genes (Ma et al., 2016). These pectin oligomers with a DP of seven to 15 applied on *Medicago sativa* L. seedlings also promoted root growth (Camejo et al., 2010). The oligomers with a DP around eight applied on *Celosia argentea* L. seedlings promoted shoot growth (Suzuki et al., 2002).

As a plant-innate elicitor, pectin-derived oligogalacturonides are the best characterized DAMPs. Their exogenous application could trigger PAMP-triggered immunity (PTI) responses including ET synthesis, inhibition of auxin action, accumulation of phytoalexins and callose, and production of ROS and NO (Howlader et al., 2020; Wang et al., 2022).

2.2 | Glycoproteins

2.2.1 | Bacterial glycoproteins

Glycoproteins consist of carbohydrates covalently linked to proteins. Bacterial glycoproteins can be classified into five major types: (1) the surface-layer glycoproteins present in the outer most macromolecular monolayer of a bacterial cell envelope, (2) membrane–associated glycoproteins, distributed in the outer/inner membrane and in the periplasmic space of the bacteria, (3) cell-surface glycoproteins associated with pili or flagella, (4) secreted glycoproteins and exo-enzymes, and (5) cellular glycoproteins (Upreti et al., 2003). The most well-known bacterial glycoprotein is peptidoglycan (PGN), also called murein. It is present in almost all prokaryotic cell walls, except those of Archaea, and contributes to the shape of bacteria. It consists of a conserved glycan backbone of *N*-acetylglucosamine or *N*-acetylmuramic acid, cross-linked by short peptides, containing two to five amino acids like L-alanine, D-glutamate, a dibasic amino acid, and D-alanine (Figure 2; Irazoki et al., 2019).

No study has dealt with PGN or other bacterial glycoproteins as biostimulants. However, it is well known that PGN is considered a MAMP in many plant species such as *A. thaliana*, rice, and tobacco, because it induces immune responses including an increase in cytoplasmic Ca^2, accumulation of ROS and NO, camalexin production and post-translational induction of MAPK activities (Gust, 2015).

2.2.2 | Fungal glycoproteins

The number of glycans present in glycoproteins differs greatly from one to more than 100 (Coté et al., 2008). *N*- and *O*-linked glycans are the most common forms of glycosylation in eukaryotic organisms. *N*-glycans are linked to proteins via the amide group of an asparagyl residue, and *N*-acetylglucosamine (GlcNAc) is found as the reducing terminal carbohydrate residue. *O*-glycans are linked to proteins via the hydroxy group of serine, threonine, and hydroproline. *O*-linked glycans feature a variety of terminal residues such as *N*-acetylgalactosamine, fucose, glucose, GlcNAc, xylose, galactose, arabinose, and *O*-linked mannose. In fungi, *N*-glycans contain mainly mannose residues, which are sometimes phosphorylated. Occasionally, residues such as galactose, pyruvate, galactofuranose, and β-1,2-linked mannose are also found. For fungal *O*-glycans, the situation is more variable, but *O*-linked mannosylation seems to be a typical feature (Coté et al., 2008).

Only glomalin, produced by hyphae and spores of arbuscular mycorrhizal fungi (AMF), has a documented biostimulant activity. Indeed, glomalin-related protein applied by foliar spray to oranges (*Citrus sinensis* L.) improved soil fertility and fruit quality (Liu et al., 2022; Meng et al., 2021) and increased drought tolerance (Chi et al., 2018) and plant growth (Liu et al., 2021). Fungal glycoproteins from *Fusarium oxysporum* and *Alternaria burnsii* (respectively with molecular weight of 29 kDa and a 14 kDa) are also known as active elicitors, able to trigger immune responses in plants such as the accumulation of antioxidative enzymes and the synthesis of different phenolics and phytoalexins (Patel et al., 2020). Oligandrins, which are glycoproteins of fungus-like microorganisms (oomycetes) are also able to induce disease resistance in plants (Benhamou et al., 2001).

2.2.3 | Seaweed glycoproteins

Only Chlorophyta exhibited hydroxyproline-rich glycoproteins (HRGPs) with characteristics like those from land plants. Arabinogalactan proteins (AGPs), extensins (EXTs), and extensin-like glycomolecules (pherophorins) have been detected and isolated from the protein-rich walls of green algae (Estevez et al., 2008). AGP-like structures were reported to

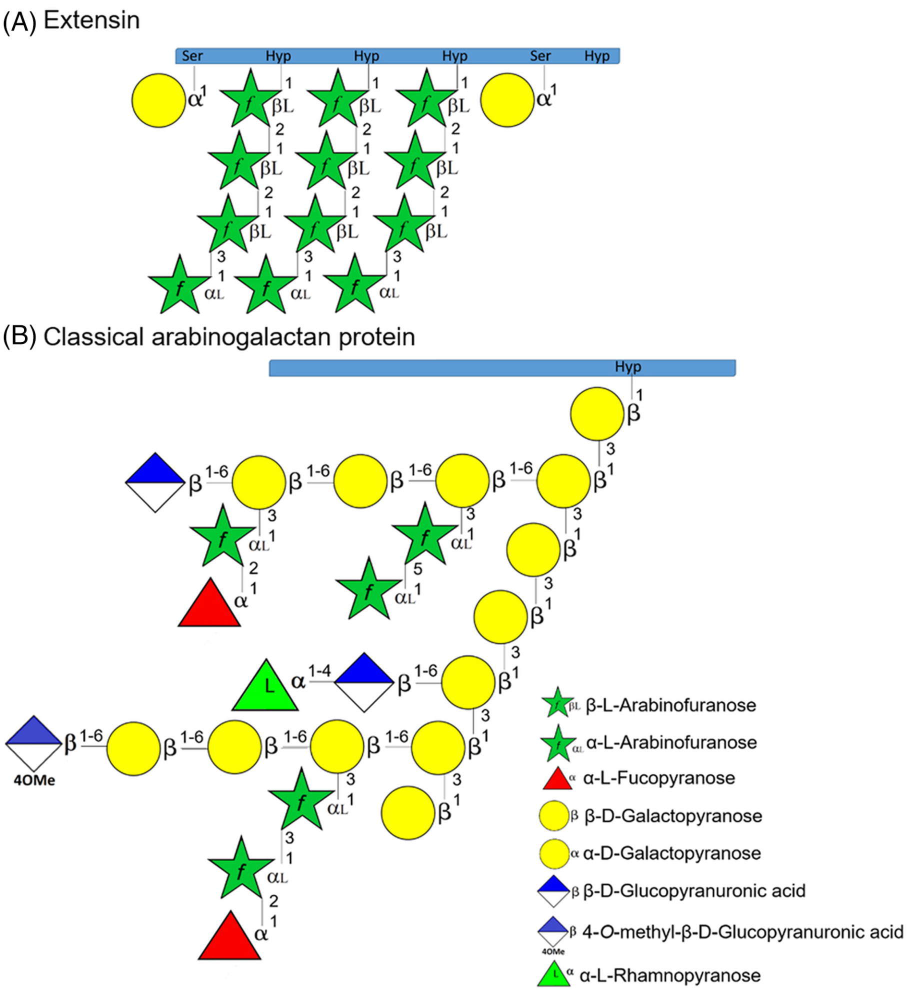


FIGURE 9 O-glycan structures of hydroxyproline-rich GlycoProteins (HRGP) from moderately glycosylated extensin to heavily glycosylated ArabinoGalactan Protein (AGP). Glycosylation of tomato extensin described by Carpita et al., (2015) and Showalter and Basu (2016). Type-II arabinogalactan structure of a classical AGP according to Nguema-Ona et al., (2012) and Showalter and Basu (2016). A GlyceroPhosphatidyl Inositol (GPI) anchor can be found in the N-terminal region of the protein but is not represented here. Abbreviations: Hyp, Hydroxyproline; Ser, Serine. Monosaccharides are represented according to the Symbol Nomenclature for Glycans (SNFG; Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

also occur in brown algae (Hervé et al., 2016). No study implicating algal glycoproteins with biostimulant activities was found, and only one recent study dealt with plant elicitor properties of this glycomolecule. Indeed, an AGP-like enriched fraction from *Ulva lactuca* induced resistance to a fungal pathogen and triggered defense mechanisms like H_2O_2, SA, and ET signaling in *Brassica napus* L. (Přerovská et al., 2022).

2.2.4 | Land-plant glycoproteins

N-glycoproteins and *O*-glycoproteins are two types of glycomolecules assembled and modified in the endoplasmic reticulum and Golgi apparatus before their transport within or outside the cell (Nguema-Ona et al., 2014). *N*-glycoproteins contain plant specific glycoepitopes such as a core β-(1,2)-xylose, core α-(1,3)-fucose residues, and possibly a Lewis antenna.

O-glycoproteins are considered HRGPs and HRGPs are commonly divided into three major multigene families: AGPs, EXTs, and pro-rich proteins (PRPs). The common feature that defines this diverse family is the hydroxylation of Proline to Hydroxyproline (Hyp) and the subsequent attachment of *O*-linked glycans on Hyp residues (Figure 9; Johnson et al., 2017). The HRGPs range from highly glycosylated molecules, such as AGPs, to the moderately glycosylated EXTs and minimally glycosylated PRPs (Nguema-Ona et al., 2014).

In terms of biostimulation, AGP-rich extracts applied in the culture medium improved the differentiation of microspores derived from embryos of *T. aestivum* (Letarte et al., 2005). They enhanced the organogenesis of guard protoplast-derived callus and increased the number of shoots formed in *Beta vulgaris* L. (Wiśniewska and Majewska-Sawka, 2007). They also reduced cell mortality and increased the frequency of mitotic divisions of microspores and the number of multicellular structures of *H. vulgare* (Makowska et al., 2017). When gum arabic, a very well-known AGP-like molecule, was added to cell suspension cultures of *V. vinifera* it promoted cell growth (Cai et al., 2011). Derivatives of gum arabic from *Acacia senegal* (L.) Britton. incorporated in culture substrates significantly improved the growth of *Catharanthus roseus* (L.) G. Don in the number of leaves, height, and dry matter production (Ali et al., 2016).

There is now scientific evidence that AGPs are involved in plant growth, development, and reproduction and in response to biotic and abiotic stress (Mareri et al., 2018), very few studies have shown their ability to function as elicitor or biocontrol compounds. Cai et al., (2011) showed that gum arabic included in cell suspension cultures of *V. vinifera* promoted the accumulation of phenolics. Cannesan et al., (2012) showed that AGPs extracted from pea root caps were able to prevent in vitro zoospore germination of the oomycete *Aphanomyces euteiches*.

2.3 | Glycolipids

2.3.1 | Bacterial glycolipids

Glycolipids are composed of carbohydrates with a hydrophilic moiety bound to lipids which are hydrophobic (Figure 10). Bacterial glycolipids are classified into 10 groups: lipopolysaccharides (LPS), rhamnolipids, rubiwettins, trehalolipids, other glycosylated mycolates, oligosaccharide lipids, glycosylated fatty alcohols, glycosylated macrolactones/−lactams, glycocarotenoids/−terpenoids, and glycosylated hopanoids (Abdel-Mawgoud and Stephanopoulos, 2018).

The most well-known bacterial glycolipids are LPS, rhamnolipids, and trehalolipids. All of them are well-recognized industrial substances whose applications are presented below.

LPS are glycolipids, found in gram-negative bacteria, composed of three structural domains: an acylated β-1′-6-linked glucosamine disaccharide called the lipid A, the core oligosaccharide usually containing 3-deoxy-D-manno-2-octulosonic acid (Kdo) residues, heptoses, and various hexoses, which can be modified with phosphates and other substituents such as phosphoethanolamine, and an extended polysaccharide composed of a repeating oligosaccharide made of two to eight sugars called the O-antigen (Bertani and Ruiz, 2018).

LPS, otherwise also known as endotoxins, are widely used for medical, food, cosmetic, and environmental diagnostics (Stromberg et al., 2017). Agricultural applications have been studied less, but some studies have indicated biostimulant activities. Indeed, LPS isolated from *Rhizobium leguminosarum* bv. trifolii applied on seedlings of red clover (*Trifolium pretense* L.) showed an increase of plant yield (Głowacka et al., 2014). Those isolated from *Azospirillum brasilense* Sp245 applied by foliar spray on wheat (*T. aestivum*) increased leaf length, spike formation, and dry weight and accelerated plant growth (Chávez-Herrera et al., 2018). LPS also act as PAMPs in plants by triggering typical pattern-triggered immunity (PTI) responses inducing the oxidative burst, NO production, Ca^{2+} influx, accumulation of PR gene transcripts, and cell-wall alterations that include deposition of callose and phenolics (Chaliha et al., 2018; Silipo et al., 2010).

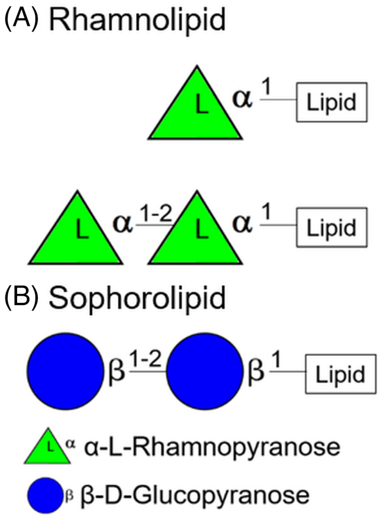


FIGURE 10 Structure of two glycolipids: rhamnolipid, mono and bi-rhamnosylated lipids found in bacteria from diverse phylums (Abdel-Mawgoud et al., 2010) and sophorolipid that can be O-acetylated on the C6 and are found in many yeasts (Cho et al., 2022). Monosaccharides are represented according to the SNFG nomenclature (Varki et al., 2015) using the Polys Glycan builder monosaccharides (https://glycan-builder.cermav.cnrs.fr/).

Rhamnolipids contain a hydrophilic group, consisting of either one or two L-rhamnose residues, with a glycosidic linkage to the hydrophobic group made up of one or two β-hydroxy fatty acids (Figure 10). They are isolated from different strains of the *Pseudomonas*, *Burkholderia*, or *Acinetobacter* genera.

Very few of them were studied in biostimulant applications. However, one study dealt with rhamnolipid 90 isolated from *Pseudomonas aeruginosa* applied on the soil of spring barley (*H. vulgare*) that was demonstrated to be an effective biostimulant of soil enzyme activities like dehydrogenases, arylsulphatase, and β-glucosidase (Zaborowska et al., 2020). Another study showed that application of rhamnolipids and EPS on seeds of *Z. mays*, *Lupinus luteus* L., *Pisum sativum* L., *Avena sativa* L., and *Sinapsis alba* L. stimulated seed germination and plant growth (Krawczynska et al., 2012). In addition, these glycolipids have several industrial applications including as emulsifiers, spreaders, dispersing agents, and recently as potential agents of bioremediation of contaminated soils (Celligoi et al., 2020; Chong and Li, 2017). They are also used as pest control, biocontrol agents against several phytopathogens, and stimulants for plant immunity. As a plant-immunity elicitor, rhamnolipids induce accumulation of ROS, Ca^{2+} influx, phosphorylation cascades, callose deposition, hormone production, defense-gene activation, and a hypersensitive reaction-like response (Crouzet et al., 2020).

Trehalolipids contain a non-reducing disaccharide in which the two glucose units are linked in an α,α-1,1-glycosidic linkage. They are produced by *Arthrobacter* sp., *Corynebacterium* sp., *Mycobacterium* sp., *Nocardia* sp., and *Rhodococcus erythropolis*. Like the other biosurfactants, they are widely used in many industrial sectors such as petroleum, food, pharmaceuticals, and agriculture. However, despite their antimicrobial properties, to our knowledge, no study has dealt with their application as biostimulants or plant-defense elicitors (Paulino et al., 2016).

2.3.2 | Fungal glycolipids

Glycolipids of fungi are classified into 10 groups: mannosylerythritol lipids (MELs), sophorolipids (Figure 10), cellobiose lipids, glucosyl-di-xylosyl lipids (glykenins), polyol fatty acid esters, glucosyl and mannosyl lipids, glycosylated polyketides, glucosyl-galactosyl lipids, glycosylated sterols, and glycosylated paraconic acids (Abdel-Mawgoud and Stephanopoulos, 2018).

As bacterial glycolipids (see Section 2.3.1), several of them are well-known industrial compounds used as biosurfactants and bioemulsifiers and recently as potential agents of bioremediation of contaminated soils (Celligoi et al., 2020).

To the best of our knowledge, only sophorolipids (Figure 10; mainly produced by yeasts) have been reported for their biostimulant activities. In agricultural applications, sophorolipids were first studied as antimicrobial agents against several plant pathogens (Celligoi et al., 2020; Chen et al., 2020). Other recent studies have shown that soil application of these glycolipids improves the growth of *M. sativa* and *Bidens Pilosa*, reduces the Cd stress, and improves soil microbial activities (Shah and Daverey, 2021).

MELs also have antimicrobial activity against phytopathogens and seem to have promising biostimulant activities by improving soil quality, contributing to plant nutrition, and stimulating plant growth (Matosinhos et al., 2022).

2.3.3 | Seaweed glycolipids

Three major types of glycolipids are found in seaweeds and marine grasses: monogalactosyldiacylglycerides (MGDGs), digalactosyldiacylglycerides (DGDGs), and sulfoquinovosyldiacylglycerides (SQDGs). MGDGs and DGDGs contain galactose linked to the sn-3 position of the glycerol backbone. SQDGs contain 6-deoxyglucose (quinovose) with a sulfonic group in the 6-position (Khotimchenko, 2002; Plouguerné et al., 2014).

To date, no published study has dealt with algal glycolipids as biostimulants or any other agricultural use. On the other hand, these glycolipids have several medical and biological activities such as antibacterial, anti-tumor, antiviral, anti-inflammatory, and antioxidant properties (Plouguerné et al., 2014). Moreover, in algal metabolism, they play an important role for energy supply and cell protection against stresses such as osmotic and salt stresses (Terme et al., 2021).

2.3.4 | Land plant glycolipids

Glycolipids play an important role in chloroplast development and morphology. Sterylglucosides (SGs), acylated sterylglucosides (ASGs), MGDGs, and DGDGs are the glycolipids contained in higher plants. Like seaweeds, MGDGs and DGDGs are major plant glycolipids and represent nearly 80% of the membrane lipids in chloroplasts. But small quantities of them are also found in non-photosynthetic plastids such as chromoplasts and amyloplasts (Kalisch et al., 2016; Rahim et al., 2018).

No formal study has explored plant glycolipids as biostimulants or in any other agricultural use. Moreover, in the metabolism of higher plants, these glycolipids ensure protection against abiotic stresses such as drought and salinity (Ge et al., 2022; Mohamed et al., 2018). MGDGs and DGDGs are also known for their role in mediating the systemic acquired resistance (SAR) process of plant defense (Chaliha et al., 2018).

All the glycomolecules like polysaccharides, glycoproteins, and glycolipids exhibiting biostimulant activities are summarized in Table 2.

As discussed above, glycomolecules often present both biostimulant and plant-immunity activities. Therefore, it is tempting to draw a parallel between sweet immunity and biostimulation.

3 | SWEET IMMUNITY VS. SWEET BIOSTIMULATION: HOW DIFFERENT ARE THE TWO ACTIVITIES?

As described in the first part of this review, many glycomolecules are involved in plant immunity. This has led to the concept of sweet immunity, which postulates that elements of sugar metabolism and signaling play critical roles in enhancing plant immune responses (Bolouri Moghaddam and Van den Ende, 2012; Chaliha et al., 2018; Trouvelot et al., 2014). Some authors have claimed that although a distinction must be made between stimulation of plant immunity and biostimulation, signaling pathways may be interconnected, and both effects may practically result from the application of the same inducers (du Jardin, 2015). Experimental evidence, reviewed above, showed that glycomolecules are used not only to inhibit the growth of pathogens, stimulate production of hormone-like substances, and reduce disease symptoms but also to enhance plant growth, nutrient uptake, and environmental stress tolerance. These effects can be analyzed at different levels: agronomical and morphological, tissue specific, on a cellular and molecular level. Thus, because the effects of elicitation of plant defense are very close to those of biostimulation, we compare the modes of action at the three levels (agronomical/ morphological, tissue/ cellular and molecular) for the sweet biostimulants and elicitors described in this review (Table 3).

At the agronomical and morphological level, it is the whole plant that is studied. For biostimulant products, this is the most common level of observation. Indeed, the most important effect of plant biostimulants from the agronomic point of view is the stimulation of crop production in quantity and quality. These effects are studied during critical stages of crop development like seed germination, plant growth, flowering, and fruiting and under different environmental conditions e.g. nutrient uptake and abiotic stress tolerance (Wozniak et al., 2020). For stimulation of plant immunity, this level is rarely studied because plant growth and immunity pathways are usually considered as antagonistic because trade-offs between plant growth and immunity often occur due to the cost of both and a limitation in plant resources (Ning et al., 2017). However, much progress has been made to understand the mechanisms of these trade-offs. Some defense-related mechanisms are known to mediate resistance against diseases without affecting crop-yield reduction (Wang et al., 2020).

As mentioned above, glycomolecules are known to operate at this level (Table 3). Indeed, bacterial glycolipids like rhamnolipids, fungal polysaccharides like chitosan and chitin, algal polysaccharides e.g. laminaran, alginates and oligo-alginates, and ulvans, and land-plant polysaccharides like pectins and derived oligosaccharides all impact seed germination.

TABLE 2 Biostimulant activities of glycomolecules. Abbreviations of biostimulant activities: Nutrient Efficiency (NE), effect on Rhizosphere (RZ), plant Quality Traits (QT) and/or abiotic Stress Tolerance (ST). EPS (exopolysaccharides); AGP (arabinogalactan proteins); LPS (lipopolysaccharides).

	Glycomolecules	Biostimulant activities (NE, RZ, QT or ST)	Target plants	Type of application	References
Polysaccharides	EPS Gellan gum and oligogellan Chitosan Chitin Laminaran Paramylon Alginate and oligoalginates Ulvan Fucoidan Carrageenan Agar Microalgal polysaccharides Cellulose and oligomer Oligoxyloglucans Xylo-oligosaccharides Pectins and derived oligosaccharides	QT QT, ST QT, RZ NE, QT, ST NE, RZ, QT, ST NE, RZ, QT, ST QT, ST QT QT QT, ST QT NE ST ST QT NE ST ST, QT QT ST RZ QT QT, ST ST ST, QT RZ, QT RZ QT, NE QT QT QT	*Zea mays, Lupinus* *luteus, Pisum sativum,* *Avena sativa, Sinapsis* *alba* *Helianthus annuus* *Cajanus cajan* *Eucomis bicolor, E.* *comosa, Perilla* *frutescens* *Cynara scolymus,* *Ocimum basilicum,* *Phaseolus vulgaris,* *Lactuca sativa,* *Hibiscus esculentus,* *Solanum tuberosum,* *Solanum lycopersicum,* *Capsicum annuum* *Brassica oleracea,* *Lactuca sativa,* *Cajanus cajan,* *Solanum lycopersicum* *Trifolium repens,* *Lolium perenne* *Arabidopsis thaliana* *Daucus carota,* *Lactuca sativa,* *Cichorium intybus* *Triticum aestivum* *Solanum lycopersicum* *Solanum lycopersicum* *Triticum aestivum* *Cucumis sativus* *Eucomis autumnalis* *Triticum aestivum* *Solanum lycopersicum* *Zea mays* *Lactuca sativa* *Daucus carota* *Oryza sativa* *Hordeum vulgare* *Arabidopsis thaliana* *Medicago truncatula* *Triticum aestivum* *Pisum sativum* *Zea mays* *Zea mays* *Triticum aestivum* *Vigna radiata,* *Foeniculum vulgare,* *Zea mays, Eucalyptus* *globulus., Arachis* *hypogaea, Nicotiana* *tabacum, Ocimum* *basilicum,* *Pinus radiata* *Cymbopogon flexuosus* *Amaranthus viridis* *Brassica oleracea*	Seed coating Seed coating Seed coating Bulb coating Plant drenching Seed, fruit and flower coating, foliar spraying, culture substrate incorporation Foliar spraying, culture substrate incorporation; fruit and flower coating Culture substrate incorporation Culture substrate incorporation Foliar spraying Culture substrate incorporation Culture medium incorporation Foliar spraying Culture substrate incorporation Bulbs coating Seed coating Culture substrate incorporation Culture substrate incorporation Foliar spraying and culture substrate incorporation Foliar spraying and culture substrate incorporation Foliar spraying Seed coating and/or foliar spraying Substrate incorporation Culture substrate incorporation Seed coating Foliar spraying Culture substrate incorporation Culture substrate incorporation Foliar spraying Culture substrate incorporation Substrate incorporation Seed coating Fruit coating Fruit coating Seedling application	Krawczynska et al., 2012 Fatima and Arora 2021 Tewari et al., 2020 Salachna et al., 2018a; Salachna, Grzeszczuk & Mizielińska, 2019 Pichyangkura and Chadchawan 2015 Shahrajabian et al., 2021 Shahrajabian et al., 2021 Wu et al., 2016 Yvin et al., 1998 Barsanti et al., 2019 Liu et al., 2013 Li et al., 2018 Salachna et al., 2018b Ma et al., 2010 Carrasco-Gil et al., 2021 Hu et al., 2004 Iwasaki and Matsubara, 2000 Xu et al., 2003 Yang et al., 2020 Shefer et al., 2022 Briand et al., 2011 Goñi et al., 2020 Zou et al., 2021 Mukarram et al., 2021 Goñi et al., 2020 Mahusook et al., 2021 Pacheco et al., 2021 Rachidi et al., 2020 El-Naggar et al., 2020 El Arroussi et al., 2018 Wei et al., 2019 Souza et al., 2017 González-Pérez et al., 2012, 2018 Páez-Watson et al., 2020 Salvador and Lasserre 2010 Chen et al., 2012 Chen et al., 2015

(Continues)

TABLE 2 (Continued)

	Glycomolecules	Biostimulant activities (NE, RZ, QT or ST)	Target plants	Type of application	References
			Solanum lycopersicum *Triticum vulgare* *Phaseolus vulgaris* *Solanum lycopersicum* *Oryza sativa* *Arabidopsis thaliana* *Arabidopsis thaliana* *Nicotiana tabacum* *Vitis vinifera, Actinidia deliciosa* *Solanum lycopersicum* *Brassica rapa* *Glycine max* *Triticum aestivum* *Vitis vinifera* *Solanum lycopersicum* *Medicago sativa, Celosia argentea*		Hassan et al., 2019 Li et al., 2021 Villegas et al., 2016 Ma et al., 2016 Camejo et al., 2010; Suzuki et al., 2002
Glycoproteins	Fungal *N*-linked glycoproteins (glomalin-related soil protein) AGPs and plant gum polysaccharides	RZ, QT, ST QT QT, RZ QT	*Citrus sinensis* *Triticum aestivum* *Beta vulgaris* *Hordeum vulgare* *Vitis vinifera* *Abelmoschus esculentus* *Catharanthus roseus*	Foliar spray Culture substrate incorporation Seed coating, Culture substrate incorporation Culture substrate incorporation	Meng et al., 2021 Liu et al., 2022 Chi et al., 2018 Liu et al., 2021 Letarte et al., 2005 Wiśniewska & Majewska-Sawka 2007 Makowska et al., 2017 Cai et al., 2011 Shobana et al., 2022 Ali et al., 2016
Glycolipids	LPS Rhamnolipids Sophorolipids	QT RZ QT QT, RZ, ST	*Trifolium pretense* *Triticum aestivum* *Hordeum vulgare* *Zea mays, Lupinus luteus, Pisum sativum, Avena sativa, Sinapsis alba* *Medicago sativa* *Bidens Pilosa*	Seedling application Seedling application and foliar spray Soil application Seed coating Soil application	Głowacka et al., 2014 Chávez-Herrera et al., 2018 Zaborowska et al., 2020 Krawczynska et al., 2012 Shah and Daverey 2021

The growth of plants was shown to be enhanced by a number of different glycomolecules derived from bacteria, including exopolysaccharides (EPS), gellan gum and oligo-gellan, lipopolysaccharides (LPS), and rhamnolipids. Similarly, fungi also produce a range of glycomolecules that can promote plant growth, including chitosan, chitin, fungal glycoproteins, and sophorolipids. Algae also produce a variety of glycomolecules that can support plant growth, including laminaran, ulvans, agar, starch, and laminaran. Land plants have been shown to produce oligomers of cellulose, oligoxyloglucans, xylooligosaccharides, pectins and derived oligosaccharides, and AGP-rich extracts able to enhance plant growth. These glycomolecules from bateria, fungi, seaweeds and land plant are also able to stimulate flowering and fruiting in plants.

The uptake of nutrients appears to be influenced exclusively by polysaccharides derived from bacteria (gellan gum and oligo-gellan), fungi (chitosan and chitin), algae (ulvans, carrageenans, and microalgal polysaccharides), and land plants (pectins and derived oligosaccharides).

Additionally, the following categories of glycomolecules (form bacterial, fungal, algal and land-plant origins) have been identified as having abiotic stress-mitigating properties: EPS, gellan gum, and oligo-gellan, chitosan, chitin, fungal glycoproteins, sophorolipids, laminaran, alginates and oligo-alginates, ulvans, fucoidans, carrageenans, agar, microalgal polysaccharides, oligoxyloglucans and xylooligosaccharides.

At the tissue and cellular level (Table 3), the indicators commonly observed for biostimulant activities are "membrane stability,"

TABLE 3 Biopreparations (with sweet immunity and sweet biostimulation) at different levels: phenological, tissular/cellular and molecular levels. In red, land plant polysaccharides considered as one of the most promising group but the less studied in terms of molecular mechanisms of glycostimulation. Abbreviations: ABA (Abscisic acid); AGP (arabinogalactan proteins); APX (ascorbate peroxidase); CAT (catalase); EPS (exopolysaccharides); ET (ethylene); (GR) glutathione reductase; JA (jasmonate); LOX (lipoxygenase); LPS (lipopolysaccharides); PAL (phenylalanine ammonia-lyase); PGN (peptidoglycans); POD (peroxidase); PPO (polyphenol oxidase); SA (salicylate); SOD (superoxide dismutase).

Level	Sweet Immunity activities	Sweet Biostimulant activities
Agronomical/ morphological 1. Seed germination 2. Plant growth 3. Flowering and fruiting 4. Nutrient Uptake 5. Abiotic stress tolerance	**No data**	1. rhamnolipids, chitosan, chitin, laminaran, alginates and oligo-alginates, ulvans, **pectins and derived oligosaccharides** 2. EPS, gellan gum and oligo-gellan, LPS, rhamnolipids, chitosan, chitin, laminaran, ulvans, agar, starch, fungal glycoproteins, sophorolipids, laminaran, alginates and oligo-alginates, ulvans, carrageenans, agar, microalgal polysaccharides, **oligomers of cellulose, oligoxyloglucans, xylooligosaccharides, pectins and derived oligosaccharides**, AGP-rich extracts 3. alginate and oligoalginates, xylooligosaccharides, fungal glycoproteins, **xylooligosaccharides** 4. gellan gum and oligo-gellan, chitosan, chitin, ulvans, carrageenans, microalgal polysaccharides, **pectins and derived oligosaccharides** 5. EPS, gellan gum and oligo-gellan, chitosan, chitin, fungal glycoproteins, sophorolipids, laminaran, alginates and oligo-alginates, ulvans, fucoidans, carrageenans, agar, microalgal polysaccharides, **oligoxyloglucans, xylooligosaccharides**
Tissular/Cellular 6. Membrane Stability 7. Production of specialized Metabolites 8. Production of Plant Growth Regulators 9. Photosynthetic Pigments and Photosynthesis	6. **No data** 7. bacterial and fungal D-glucans, rhamsan, PGN, LPS, chitosan, fungal glycoproteins, starch, alginates and oligo-alginates, **oligomers of cellulose**, AGP-rich extracts 8. EPS, rhamnolipids, laminaran, ulvans, fucoidans, carrageenans, algal AGP-like fraction, **xyloglucans, xylooligosaccharides, pectins and derived oligosaccharides** 9. **No data**	6. **oligoxyloglucans, xylooligosaccharides** 7. gellan gum and oligo-gellan, alginate, carrageenans, chitosan, **oligoxyloglucans** 8. alginates and oligo-alginates 9. gellan gum and oligo-gellan, alginates and oligo-alginates, microalgal polysaccharides, **oligoxyloglucans, pectins and derived oligosaccharides**
Molecular 10. Reactive Oxygen Species (ROS) 11. Nitric oxide (NO) 12. Mitogen-activated protein kinases (MAPK) 13. Ca2+ signaling 14. SA and ET/JA-mediated signaling pathways 15. Others phytohormones (abscisic acid (ABA), auxins and cytokinins) 16. Protein phosphorylation 17. Antimicrobial (phytoalexin, defensin,…) 18. Pathogenesis-related protein (PR protein)	10. EPS, PGN, LPS, rhamnolipids, chitosan, laminaran, alginates and oligo-alginates, ulvans, microalgal polysaccharides, **oligomers of cellulose, xylooligosaccharides, arabinoxylan-oligosaccharides and mixed-linked glucans, oligomannans, pectins and derived oligosaccharides** 11. PGN, LPS, chitosan, alginates and oligo-alginates, **xylooligosaccharides, pectins and derived oligosaccharides** 12. PGN, chitin, **oligomers of cellulose, xyloglucans, arabinoxylan-oligosaccharides and mixed-linked glucans, oligomannans** 13. PGN, LPS, rhamnolipids, laminaran, microalgal polysaccharides, **oligomers of cellulose, arabinoxylan-oligosaccharides and mixed-linked glucans, oligomannans** 14. EPS, rhamnolipids, laminaran, ulvans, fucoidans, carrageenans, algal AGP-like fraction, **xyloglucans, xylooligosaccharides, pectins and derived oligosaccharides**	10. **laminaran** 11. **No data** 12. **No data** 13. **No data** 14. **No data** 15. alginates and oligo-alginates 16. **No data** 17. **No data** 18. **No data** 19. alginates and oligo-alginates, **oligoxyloglucans, xylooligosaccharides** 20. **pectins and derived oligosaccharides**

(Continues)

TABLE 3 (Continued)

Level	Sweet Immunity activities	Sweet Biostimulant activities
19. Antioxidant enzymes (SOD, CAT, APX, POD, GR, …) 20. Phenylpropanoids pathways (PAL, PPO, LOX,…)	15. rhamnolipids, **pectins and derived oligosaccharides** 16. PGN 17. bacterial and fungal D-glucans, rhamsan, chitosan, fungal glycoproteins, laminaran, alginates and oligo-alginates, ulvans, fucoidans, **xyloglucans, pectins and derived oligosaccharides** 18. LPS, rhamnolipids, fungal D-glucans, chitosan, chitin, laminaran, fucoidans, **oligomers of cellulose, xyloglucans** 19. xanthan, fungal glycoproteins, alginates and oligo-alginates, ulvans, microalgal polysaccharides, **fructans** 20. bacterial and fungal D-glucans, chitin, fucoidans, microalgal polysaccharides	

"production of secondary metabolites," "production of plant growth regulators," and "photosynthetic pigments and photosynthesis" (Van Oosten et al., 2017). Regarding glycomolecules, polysaccharides from algae and land plants e.g. oligoxyloglucans and xylooligosaccharides, were reported to have a positive effect on membrane stability while no data was reported in plant-defense studies. Production of specialized metabolites seemed to be induced by both activities for glycomolecules from bacterial, fungal, algal, and land-plant origins. For the "production of plant growth regulators" indicator, only alginates and oligo-alginates were reported to have an effect in sweet biostimulant activities. In contrast, this indicator is commonly reported during elicitation in the process of sweet immunity. Interestingly, the indicator "photosynthetic pigments and photosynthesis," which is well described for several glyco-biostimulants, seems to be absent from reports related to sweet immunity.

Lastly, the molecular level (Table 3) is the most common level observed for glycomolecules involved in plant immunity where they classically activate ROS, NO, MAPK, Ca^{2+} signaling, SA and ET/JA-mediated signaling pathways, other phytohormones like ABA, auxin, cytokinins, etc., protein phosphorylation, antimicrobial compounds, PR proteins, antioxidant enzymes, and the phenylpropanoids pathway. In contrast, it is the less studied level for glycomolecules involved in biostimulant activity and for biostimulants in general (Xu et al., 2020). Indeed, few glycomolecules have been investigated at this level. Alginates and oligo-alginates seemed to enhance the production of antioxidant enzymes and phytohormones such as ABA, auxin, or cytokinins. Oligoxyloglucans and xylooligosaccharides also influenced antioxidant enzyme production. The phenylpropanoid pathway seemed to be activated by pectins and pectin-derived oligosaccharides.

Thus, the review leads us to conclude that glycomolecules have a continuum of responses from the molecular level, mainly provided by studies on sweet immunity, to the agronomical and morphological levels, mainly provided by studies on sweet biostimulation. Furthermore, land-plant polysaccharides appear to be one of the most promising classes of glycomolecules, present at all levels (Table 3). However, they have been less studied in terms of the molecular-level mode of action in glycostimulation.

4 | GLYCOSTIMULATION'S MODE OF ACTION?

Focusing on land-plant polysaccharides and according to the data summarized in Table 3, we can propose the hypothetical modes of action of land-plant polysaccharides as biostimulants (Figure 11).

Land-plant polysaccharides applied to plants can penetrate the hydrophobic cuticles when they have low molecular weights. However, when they have high molecular weights, they can also enter along organ surfaces (Goñi et al., 2020). This means, the stomatal pores present in the epidermis of all aerial parts and the rhizodermis of primary roots of a few plant species such as peas, carobs, or sunflowers (Christodoulakis et al., 2002). Depending on the size and structure of those poly- or oligosaccharides, they can then be perceived by cell-surface receptors like pattern recognition receptors (PRRs), wall-associated kinases (WAKs), or FERONIA receptor kinases (FER; Swaminathan et al., 2022; Wang et al., 2022). Then, a classical intracellular signaling cascade may occur involving Ca^{2+}, NO, ROS, MAPK, antimicrobial secondary metabolites, plant hormones, PR proteins, antioxidant enzymes, and the phenylpropanoid pathway.

This signaling cascade is mainly a plant-defense signature but is also recorded in several pathways including abiotic stress tolerance and plant phenology. Moreover, several of them are interlinked.

Indeed, Ca^{2+} is an important regulator of plant development, abiotic stress tolerance, symbiotic interactions, hormone regulation, and mechanical stimulations (Batistič and Kudla, 2012). It can be involved in cell-wall remodeling via cross-linking of acidic pectin residues, in membrane stability and permeability, in enzyme secretion, and in leading changes in several other cellular events thanks to the Ca^{2+}-binding proteins (Hepler, 2005; Khan et al., 2014). It is also involved in the elevation and/or maintenance of NO generation. NO is also a multifaceted

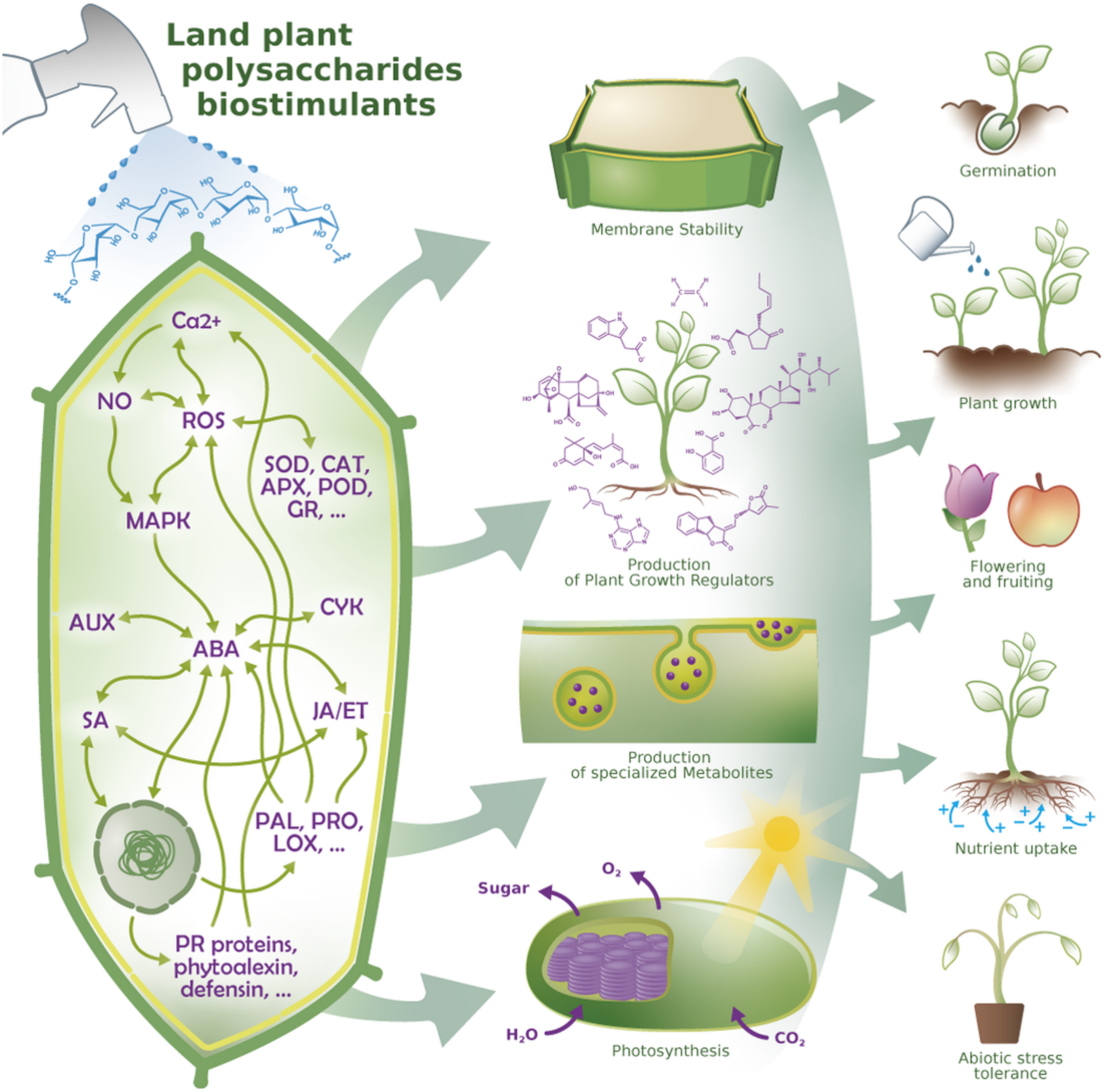


FIGURE 11 Hypothetical model of land plant polysaccharides mode of action at different levels: agronomical/morphological, tissular/cellular and molecular levels. Abbreviations: please sort them alphabetically. ABA (abscisic acid); APX (ascorbate peroxidase); GR (glutathione reductase); AUX (auxins); CAT (catalase); CYK (cytokinins); ET (ethylene); JA (jasmonate); LOX (lipoxygenase); MAPK (mitogen-activated protein kinase); NO (nitric oxide); PAL (phenylalanine ammonia-lyase); PPO (polyphenol oxidase); POD (peroxidase); ROS (reactive oxygen species); SA (salicylate); SOD (superoxide dismutase).

molecule involved in plant growth and development and in the tolerance of plants to biotic and abiotic stresses (Khan et al., 2014). ROS, are key players in biotic and abiotic stress tolerance, also act as signals in petals, pollen tubes, and gametophyte developments, in germination (Althiab-Almasaud et al., 2023), in auxin metabolism and in other hormonal pathways (Mhamdi and Van Breusegem, 2018). ROS modulate the mechanisms for propagation of Ca^{2+} by activating Ca^{2+}-dependent channels and transporters (Gilroy et al., 2016). ROS also interact with NO in direct and indirect ways. NO can directly modify ROS signaling in cellular compartments of chloroplasts and peroxisomes in chemical reactions producing reactive nitrogen species (RNS). More indirectly, induction of NO synthesis can occur by hydrogen peroxide and accumulation of ROS due to inhibition of antioxidant enzymes by NO-dependent protein modifications (Scheler et al., 2013).

Besides plant immunity, MAPK cascades activated by ROS are essential components in response to environmental stresses and in plant growth and development such as plant cytokinesis, cell division, reproduction, and root development. These functions are essentially due to their involvement in the biosynthesis and/or signaling of plant hormones like abscisic acid (ABA) signaling, auxin biosynthesis, polar transport and signaling, ET biosynthesis and signaling, JA biosynthesis and signaling, SA biosynthesis and signaling, brassinosteroid signaling, and cytokinin homeostasis and signaling (Zhang and Zhang, 2022). These hormones regulate transcription factors, which bind to gene promoters to regulate gene expression and subsequent biosynthesis of secondary metabolites. These metabolites can directly act in plant defense but also participate in ROS scavenging and abiotic stress tolerance (Meraj et al., 2020).

Other well-known defense compounds such as PR proteins are also accumulated in many plants subjected to biotic stress and act directly on pathogens and/or indirectly by acting as stimuli to trigger other pathways relevant to plant-defense mechanisms such as hormones, ROS, or Ca^{2+} pathways. PRs are also produced during plant growth and adjustments to abiotic stress such as drought, salt, cold, or heavy metals stresses (Islam et al., 2023). When the plant undergoes ROS production, the antioxidant machinery is important for protection against abiotic stress. To minimize the damaging effects, plants activate enzymatic SOD, glutathione peroxidases (GPXs), GST, glutathione reductase (GR), APX, or CAT and non-enzymatic antioxidants like ascorbic acid, glutathione, phenolics, alkaloids, flavonoids, non-protein amino acids, and α-tocopherols (Gill and Tuteja, 2010; Rajkumar et al., 2022). Similarly, in plant defense against pathogens, defense mechanisms comprise enzymatic components including those of the antioxidant machinery that regulate the steady-state level of ROS (Biswas et al., 2020). Phenolics are synthesized by the phenylpropanoid pathway thanks to its enzymatic machinery involving PAL, PPO, POD, LOX, and cinnamyl alcohol dehydrogenase (CAD), among others. As mentioned above, these have antioxidant properties but also well-established antimicrobial activities. Moreover, they are involved in major abiotic stresses, seed germination, growth, and biomass accumulation (Kumar et al., 2020; Sharma et al., 2019).

Altogether these molecular events can be connected to cellular and tissue events observed in both sweet immunity and biostimulation. Indeed, membrane stability is related to Ca^{2+}, NO, and ROS alleviation or enhancement. The production of specialzed metabolites and plant-growth regulators, including antimicrobial secondary metabolites, plant hormones, PR proteins, and phenolics, has been previously described as a factor influencing plant growth, seed germination, and abiotic stress tolerance. Moreover, photosynthesis can be linked to ROS and enzymatic and non-enzymatic antioxidants e.g. singlet oxygen, superoxide radical, H_2O_2, OH, Fe/Cu/Zn SOD, and tocopherols (Rao and Chaitanya, 2016). Finally, these tissue specific events are linked to agronomical and morphological observations classically mentioned after biostimulant applications, for example, seed germination, growth, flowering and fruiting, nutrient uptake, and abiotic stress tolerance.

In addition to the aforementioned biochemical actions, the physical properties of polysaccharides must also be considered. Indeed, The rheological and solubility properties of these substances are dependent on their molecular weight, which can be used as mentioned before, in the agronomical sector e.g., in coatings, encapsulations, nanostructures, and complexing agents. Several studies have mentioned that low molecular weight of polysaccharides increases molecular aggregation, exposing more hydroxyl groups and increasing charge-to-mass ratio, electrostatic interaction, and water binding (Wang et al., 2023).

5 | CONCLUSION

Biostimulants are promising and trendy substances as evidenced by a large body of published literature, which has considerably increased over the last decade (du Jardin et al., 2020). Glycomolecules are an encouraging class of biostimulants because they are hydrophilic, biodegradable polymers and can be used as safer "agrochemicals" (Campos et al., 2014). However, they are understudied and, like other biostimulant classes, have mainly been studied at the agronomical and morphological level. Glycomolecules as plant-defense elicitors have been aptly described in the sweet immunity concept mainly at the molecular level. Our review now enables us to offer the concept of glycobiostimulation or sweet biostimulation.

This review also encourages further study of the effects of these substances as biostimulants at a molecular level to confirm the sweet biostimulation concept and determine their precise modes of action that are currently missing. Indeed, for agrochemical products, understanding the mode of action of biostimulants is a key for greater consumer trust, quality control, certification that the product will deliver the expected results, and marketing under a regulatory framework.

It is noteworthy that the generation of a large dataset makes full elucidation of modes of action more reliable, and this includes usage of omics approaches. Omics approaches are high-throughput technologies measuring global changes in the abundance of transcriptome, proteome, metabolome, glycome, and ionome in complex biological systems because of biochemical stimulation or perturbation. Such data-driven systems are the more holistic approach to the changes taking place at multiple levels. These tools help to unravel bioactive compounds in natural and formulated products in different fields of research including medical science, toxicology, and synthetic chemical pesticides (Xu et al., 2020). Some studies on biostimulants using omics tools have already helped to enhance knowledge about the modes of action of these biosolutions (Paul et al., 2019; Ganugi et al., 2022). However, to the best of our knowledge, there has been no study on biostimulants using integrative multi-omics approaches (panomics). Some studies have combined metabolomics with phenomics (Alfosea-Simón et al., 2022; De Deigo and Spíchal, 2022; Sorrentino et al., 2022) or metabolomics and transcriptomics (Monterisi et al., 2024). However, large-scale approaches at different levels such as panomics are now essential to fully understand and characterize the modes of action of biostimulants, as several well-known experts in the field have recently recognized (du Jardin et al., 2020; Povero, 2020; Xu et al., 2020; Yakhin et al., 2017). This is a major objective for the future research on biostimulants in general and for glycomolecules as an emergent and promising category therein.

AUTHOR CONTRIBUTIONS

I.B. conceived the idea and wrote the original draft. J.C.M. conceived structures of the glycomolecules from Figure 1 to Figure 10. All authors proofread and edited the manuscript. The final version has been read and approved by all co-authors.

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DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created in this review.

ORCID

I. Boulogne https://orcid.org/0000-0001-6810-6504

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