



Review article

Carbohydrate elicitor-induced plant immunity: Advances and prospects

Birhanu Kahsay Meresa^{a,*}, Kiros-Meles Ayimut^b, Micheale Yifter Weldemichael^a, Kalayou Hiluf Geberemedhin^d, Hagos Hailu Kassegn^c, Bruh Asmelash Geberemikael^a, Etsay Mesele Egigu^a

^a Department of Biotechnology, College of Dryland Agriculture and Natural Resources, Mekelle University, Mekelle, Tigray, Ethiopia

^b Department of Crop and Horticultural Sciences, College of Dryland Agriculture and Natural Resources, Mekelle University, Mekelle, Tigray, Ethiopia

^c Department of Food Science and Postharvest Technology, College of Dryland Agriculture and Natural Resources, Mekelle University, Mekelle, Tigray, Ethiopia

^d Department of Chemistry, College of Natural and Computational Sciences, Mekelle University, Mekelle, Tigray, Ethiopia

ARTICLE INFO

Keywords:

Biocidal activities
Biotic and abiotic stresses
Carbohydrate elicitor
Environmental factors
Induced resistance
Defense responses
Structure-activity relationships
Symbiosis signaling

ABSTRACT

The perceived negative impacts of synthetic agrochemicals gave way to alternative, biological plant protection strategies. The deployment of induced resistance, comprising boosting the natural defense responses of plants, is one of those. Plants developed multi-component defense mechanisms to defend themselves against biotic and abiotic stresses. These are activated upon recognition of stress signatures via membrane-localized receptors. The induced immune responses enable plants to tolerate and limit the impact of stresses. A systemic cascade of signals enables plants to prime un-damaged tissues, which is crucial during secondary encounters with stress. Comparable stress tolerance mechanisms can be induced in plants by the application of carbohydrate elicitors such as chitin/chitosan, β -1,3-glucans, oligogalacturonides, cellodextrins, xyloglucans, alginates, ulvans, and carrageenans. Treating plants with carbohydrate-derived elicitors enable the plants to develop resistance appliances against diverse stresses. Some carbohydrates are also known to have been involved in promoting symbiotic signaling. Here, we review recent progresses on plant resistance elicitation effect of various carbohydrate elicitors and the molecular mechanisms of plant cell perception, cascade signals, and responses to cascaded cues. Besides, the molecular mechanisms used by plants to distinguish carbohydrate-induced immunity signals from symbiotic signals are discussed. The structure-activity relationships of the carbohydrate elicitors are also described. Furthermore, we forwarded future research outlooks that might increase the utilization of carbohydrate elicitors in agriculture in order to improve the efficacy of plant protection strategies.

1. Introduction

Plants are exposed to enormous biotic and abiotic stress factors during their life span. To overcome these stresses, plants have developed a multi-component immunity system. The initiation of plant defense responses depends on the accurate and timely

* Corresponding author.

E-mail addresses: birhanu.kahsay@mu.edu.et, birhanukahsay@gmail.com (B.K. Meresa).

<https://doi.org/10.1016/j.heliyon.2024.e34871>

Received 18 February 2023; Received in revised form 10 July 2024; Accepted 17 July 2024

Available online 18 July 2024

2405-8440/© 2024 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

recognition and sensing of stress signatures by plants [1]. Plants contain cell surface-localized pattern recognition receptors (PRRs), which are vital to perceive pathogen- and pest-derived pathogen-associated molecular patterns (PAMPs) and damage-associated molecular patterns (DAMPs) from the host [2,3]. The detection of conserved PAMPs/DAMPs through PRRs induces pattern-triggered immunity (PTI) as the first line of defense mechanisms to limit the growth of an invading pathogen/pest. On the other hand, plants recognize pathogen-variable effectors to induce effector-triggered immunity (ETI) which is systemic and important to confer resistance at infected tissues [4], and acquire broad-spectrum defense responses to invading phytopathogens/pests [5]. Defensive cellular activities like reactive oxygen species (ROS) burst and nitric oxide (NO) generation, cytosolic calcium ion (Ca^{2+}) influx, defense kinases activation, phytohormones production, and transcription factor (TF) activation are involved in both PTI and ETI responses [6]. The interactions of these activities are critical for amplifying immunity reactions at distal sites and thus limiting pathogen spread [7]. Additionally, plant immunity can be primed upon recognition of PAMP/DAMP/effectors or similar compounds, which is a trump card upon secondary infection [8]. Furthermore, cellular activities induced in response to both biotic and abiotic stresses share certain amount of common components [9].

The fluctuating environment and briskly adapting phytopathogens/pests could take dominance over the plant's innate immunity leading to impaired plant productivity. To improve crop productivity, numerous synthetic agrochemicals have been extensively used. These, however, are often associated with risks to environmental and human health and the emergence of resistant-strains [10]. Thus, the intensifying urge to replace synthetic agrochemicals with alternatives led to the conception of safe, eco-friendly, and cost-effective biological plant protection strategies. In this regard, carbohydrates and their respective derivatives are gradually emerging to substitute synthetic agrochemicals.

Numerous carbohydrates and their respective oligomers and monomers are potent plant immunity elicitors in different plant species used to control biotic and abiotic stresses. In plants, simple sugars such as trehalose, sucrose, and glucose are considered as important signaling molecules modulating various biological processes that also serve as defense response elicitor molecules [1,11]. With an advancement of functional glycomics, researchers are able to identify microbial cell-surface carbohydrates, including bacterial glyco-conjugates (like lipopolysaccharides (LPS), glycoproteins, and lectins) and fungal cell walls (like chitins and β -glucans) that can be recognized by the PRR and trigger plant defense responses during plant-microbe interactions [1]. Plant cell wall-originating carbohydrates such as oligogalacturonides (OGAs) and cellodextrins have also been known to act as plant defense regulators during plant-microbe interactions [12,13]. Exogenously supplied carbohydrates and their respective derivatives, originating from microbes, plants, seaweeds, and crustaceans, are perceived by the PRRs leading to the development of multi-component defense signaling routes; activated stress tolerance mechanisms such as cell-wall reinforcement, stomatal closure, phytoalexins production, ion homeostasis, and pathogenesis-related (PR) proteins synthesis [11,13,14]. Seaweed-derived carbohydrates such as alginates, ulvans, laminarins, and carrageenans are gaining much interest as new bio-elicitor materials for triggering plant defense mechanisms [1,13]. In addition, recent reports have shown that plant cell wall-originating oligomers, i.e., oligoxyloglucans [15], mannans [16], arabinoxylans [17], and β -1,3/1,4-mixed linkage glucans (MLGs) [18,19]; a polysaccharide (EPS66A) derived from an unidentified *Streptomyces* sp. [20]; microalgal polysaccharides [21]; and sulfated polysaccharides extracted from *Rugulopteryx okamurae*, a seaweed [22], are effective in triggering plant defense responses.

In recent years, advances in *omics* analytical tools have encouraged researchers to reveal the underlying mechanisms of both known and newly identified defense-associated carbohydrates in inducing plant innate immunity and their potential to defy biotic and abiotic stresses. The findings of these extensive studies revealed that carbohydrates are clearly effective in inducing robust and long-lasting defense responses in multitude of plants to control various stress factors. However, the intensity and consistency of the carbohydrate-induced plant immunity are variable according to the inducer carbohydrate structure, induced defense signaling pathway, stress factor, species of the treated plant, and extrinsic factors. Therefore, we reviewed in detail recent advances on the potential of various carbohydrate elicitors in controlling diverse plant stresses and the molecular mechanisms of plants to recognize carbohydrate elicitors, transduced signals, and responses to transduced signals. Besides, how a plant could discriminate between carbohydrate-induced immunity and symbiosis signals is discussed. The carbohydrate structure-activity relationships are also described. Finally, hot topics for further research are forwarded.

2. Carbohydrate elicitor perception system in plants

PRRs are capable of recognizing carbohydrate containing PAMPs/DAMPs released during microbe-plant interaction and could lead to the activation of plant immunity [4,23]. Similarly, PRRs can recognize an exogenously applied carbohydrate and activate networked intracellular signaling components, leading to defense elicitation [13] (Fig. 1). On the basis of the presence or absence of a cytoplasmic domain, plant PRRs could be either receptor-like proteins (RLPs) or receptor-like kinases (RLKs) [24]. RLK-PRRs usually consist of a variable extracellular domain (ECD) for binding extracellular signals, a *trans*-membrane domain important for their localization in the plasma membrane, and a conserved cytoplasmic kinase domain necessary for extracellular signal cascading [25]. RLP-PRRs, on the other hand, possess the ECD and *trans*-membrane domains but lack the cytoplasmic kinase domain [25]. For extracellular ligand recognition, the ECD of RLKs/RLPs-PRR contains either leucine-rich repeat receptors (LRR), lysin motifs (LysM), growth factor-like, malectin, or lectin motifs [26,27]. The LysM containing PRRs exist ubiquitously in most living organisms and have been widely studied for their involvement in the recognition of extracellular N-acetylglucosamine-containing ligands [8,28,29].

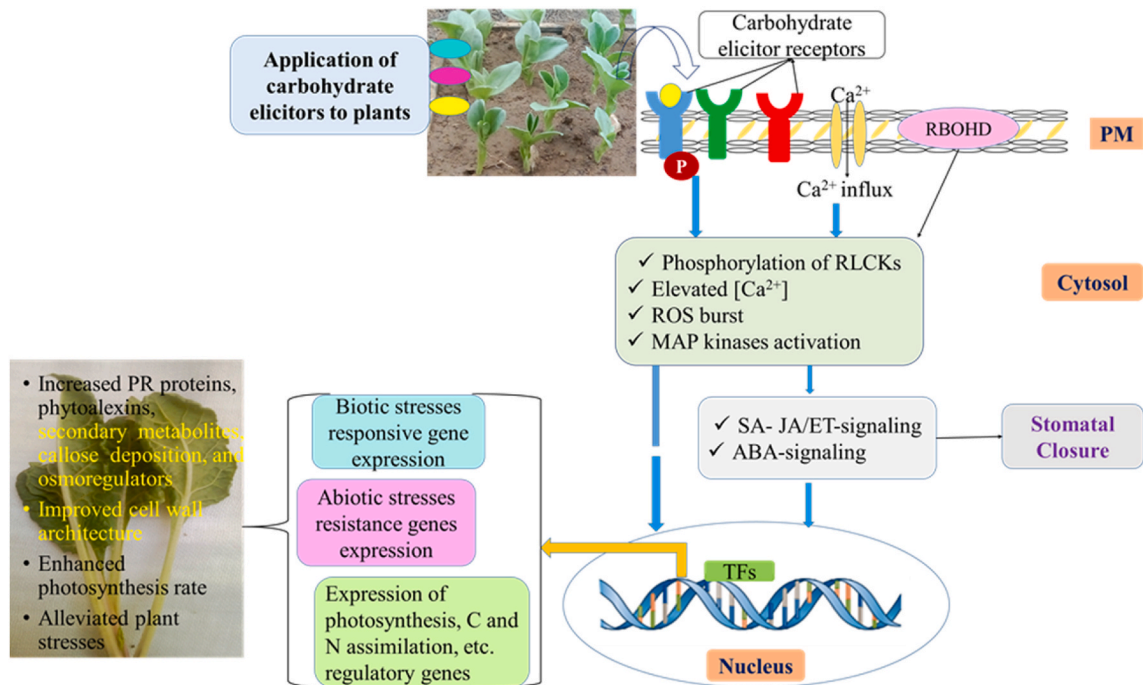


Fig. 1. A simplified schematic diagram outlining the mechanism of carbohydrates as defense responses inducer in plants. ABA, abscisic acid; JA, jasmonic acid; MAP, mitogen-activated protein; NO, nitric-oxide; PM, plasma membrane; PR, pathogenesis-related; RLCK, receptor like cytoplasmic kinase; RBOHD, respiratory burst oxidase homolog D; ROS, reactive oxygen species; SA, salicylic acid; TF, transcription factor.

2.1. *LysM-RLK/RLP receptors*

Chitin elicitor receptor kinase (CERK), a *LysM*-containing RLK, identified in monocot and dicot species, has been recognized to be essential for chitin-triggered plant immunity [30]. In rice, OsCERK1 needs to form a receptor complex with chitin elicitor binding protein (CEBiP), a *LysM*-containing RLP, to activate chitin-induced signaling [31–34]. Beside to OsCERK1 and OsCEBiP, *LysM*-containing protein 4 (LYP4) and LYP6 which are homologous to OsCEBiP, have been recognized as chitin and peptidoglycan (PGN) receptors in rice and have the potential to form a complex with OsCERK1 [35]. The dimerization of OsCEBiP with OsCERK1 facilitates the homodimerization and cytosolic phosphorylation of OsCERK1 which is required for downstream signal transduction [36]. In a recent report, CERK1 and CEBiP hetero-oligomeric receptor complex is required in the perception of rice cell wall derived MLGs [18]. Furthermore, OsCERK1 was required as receptor/co-receptor for LPS detection and for LPS-induced immune responses in rice [37]. On the other hand, OsCERK1-independent perception and induction of defense activities were observed in β -1,3-glucan-treated rice [38], indicating the diverse nature of carbohydrate receptors on the rice cell surface.

Arabidopsis thaliana (hereafter, *Arabidopsis*) has five *LysM*-containing RLKs named from LYK1 (AtCERK1) to LYK5 [39,40]. All, except LYK3 [41], are involved in activating immune responses following chitin detection in *Arabidopsis*. Both LYK5 and AtCERK1 bind directly to chitin but LYK5 showed greater affinity [36]. In response to chitin perception, LYK5 interacted with AtCERK1 and led to autophosphorylation of AtCERK1 [42], which was required for downstream defense responses activation [43]. The LYK5 transiently internalized into endocytosis to ensure proper receptor turnover [44]. LYK4 is indispensable for chitin-induced immune responses [39]. To perceive chitin, AtCERK1, LYK4, and LYK5 form a tripartite receptor complex [40]. According to Li et al. [45], the ectodomain dimerization of LYK4-LYK5 is constitutive, whereas the dimerization of AtCERK1-LYK5 is chitin-induced. LYK2 is dispensable for chitin detection but necessary for chitin-primed defense genes expression during fungal infection [46]. Notably, LYK5 and LYK4 are pseudo-kinases, and thus the kinase-active AtCERK1 is required to transduce chitin-signaling [30]. CERK1 is also involved in the perception of various carbohydrate elicitors, including PGN, β -1,3-glucan, and laminarinhexose in *Arabidopsis* [38,47,48]. In addition to regulating plant immunity against biotic stresses, AtCERK1 and LYK4 mediate chitin-induced salt and heat tolerance in *Arabidopsis* [49,50], respectively. On the other hand, over-expression of LYK4-compromised *Enterobacter* sp. SA187 (a beneficial microbe) triggered salt tolerance in *Arabidopsis* through interfering with plant ethylene homeostasis [51].

LysM-containing PPRs, involved in chitin oligomers recognition and subsequent defense signaling, were also studied in non-model plants other than rice and *Arabidopsis* (Table 1). In grapevine, VvLYK1-1 and VvLYK1-2 are orthologues of AtCERK1 and OsCERK1 and are necessary for typical defense responses following chitin and chitosan detection [52]. A very recent report indicates that cotton VvLYK5-1, an orthologue of AtLYK5, interacted with VvLYK1-1 after chito-oligosaccharides (COs) perception and induced resistance against grapevine downy mildew [53]. In response to chitin detection, PsLYK9 was found to form a receptor complex with PsLYR4, triggering signaling pathways and defensive responses in pea [54,55]. Treatment of pea with deacetylated COs resulted in differential

Table 1

List of representative plant cell surface receptor/co-receptor members involved in the recognition of immunity-inducing carbohydrate elicitors.

Receptor Type	Receptor Name	Co-receptor/s	Carbohydrate ligand/s detected	Plant species in which the receptor/co-receptor identified	Reference/s	
LysM-RLK	AtLYK5	AtCERK1	Chitin	<i>A. thaliana</i>	[42]	
	VvLYK1-1	VvLYK1-2 and VvLYK5-1	Chitin and chitosan	<i>Vitis vinifera</i>	[52,53]	
	GhLYK1 (GhCERK1)	GhLYK5	Chitin	<i>Gossypium hirsutum</i>	[57,58]	
	PsLYK9	PsLYR4	Chitin	<i>Pisum sativum</i>	[54,55]	
	SILYK1	SILYK4	Chitin	<i>Solanum lycopersicum</i>	[59,60]	
	MmLYK2	MmLYP1	Chitin	<i>Morus multicaulis</i>	[61]	
	MtLYK9	MtLYR4	Chitin	<i>Medicago truncatula</i>	[62]	
	MaLYK1	–	Chitin	<i>Musa acuminata</i>	[63]	
	CaCERK1, CaLYK4/5	–	–	<i>Coffea arabica</i>	[64]	
	MdCERK1	–	Chitin	<i>Malus domestica</i>	[65]	
	MdCERK1-2	–	Chitin	<i>M. domestica</i>	[66]	
	LysM-RLP	OsCEBiP	OsCERK1	Chitin	<i>Oryza sativa</i>	[67]
		LYP4, LYP6	OsCERK1	Chitin/PGN	<i>O. sativa</i>	[35]
LYP2, LYP 3		–	PGN	<i>A. thaliana</i>	[47]	
GbLYP1		–	Chitin	<i>G. barbadense</i>	[68]	
CaLYP		–	–	<i>C. arabica</i>	[64]	
HvCEBiP		–	Chitin	<i>Hordeum vulgare</i>	[69]	
TaCEBiP		TaCERK1	Chitin	<i>Triticum aestivum</i>	[70]	
LRR- malectin-RLK	CORK1	–	Cellotriose and cellopentose	<i>A. thaliana</i>	[71,72]	
Lectin-RLK	CaMBL1	–	Mannose	<i>Capsicum annuum</i>	[73]	
	FaMBL1	–	Mannose	<i>Fragaria ananassa</i>	[74]	
	OsLecRK1	–	MLGs	<i>O. sativa</i>	[75]	
EGF-like RLK	WAK1	BAK1	Pectin and OGA	<i>A. thaliana</i>	[76]	

BAK1, brassinosteroid insensitive 1-associated receptor kinase 1; CEBiP, chitin elicitor binding protein; CERK, chitin elicitor receptor kinase; CORK1, cellooligomer-receptor kinase 1; EGF, epidermal growth factor; LecRK1, lectine-like receptor kinase 1; LRR, leucine-rich repeat; LYP, LysM-containing protein; LysM, lysin motifs; MBL1, mannose-binding lectin 1; MLGs, mixed-linked β -1,3/1,4-glucans; OGA, oligogalacturonide; RLK, receptor-like kinases; RLP, receptor-like proteins; WAK1, Wall-associated kinase 1.

expression of genes encoding typical regulators of defense-related intracellular signal transduction pathways, which might be involved in the COs-induced signaling downstream of PsLYK9 [56].

Two LysM-containing RLKs-encoding genes in cotton, *GhLYK1* (*GhCERK1*) and *GhLYK2*, were up-regulated following chitin treatment and *Verticillium dahliae* infection, which makes them crucial in developing resistance [57]. Similar to the LYKs from Arabidopsis, all three LysM ECDs of both GhCERK1 and GhLYK2 are essential for directly detecting chitin in chitin [57]. However, GhLYK2, but not GhCERK1, is an atypical kinase, and GhLYK2 cannot interact with GhCERK1 [57]. On the other hand, the ECD of GhLYK2 is able to trigger ROS generation and cell death in a chitin-independent manner [57]. Thus, GhCERK1 and GhLYK2 might follow different pathways in contributing to cotton's defense responses. Chitin-triggered activation of mitogen-activated protein kinase (MAPK) was impaired when GhCERK1 (but not GhLYK2, GhLYK3, or GhLYK4) was silenced, and a slight but reproducible reduction in chitin-induced MAPK activation was obtained as a result of GhLYK5 silencing [58]. Compared to GhCERK1, GhLYK5 showed a higher affinity for chitin [58]. GhLYK5-GhCERK1 is a receptor complex for chitin perception in cotton. Unlike in Arabidopsis, GhCERK1 in cotton is unable to phosphorylate GhLYK5 *in vitro*; rather, GhWAK7A physically associates with GhCERK1 and GhLYK5 and facilitates chitin-induced dimerization of GhLYK5-GhCERK1 [58]. Other PRRs in cotton, including LYK7, LYP1, and extracellular LysM proteins 3 (LysMe3), play a significant role in detecting chitin signals to trigger downstream defense processes and activate cotton's resistance against *V. dahlia* [68].

Liao et al. [59] investigated the role of AtCERK1 homologs (SILYK1, SILYK12, and SILYK13) in chitin signaling in tomato. SILYK12 is involved in AM symbiosis, whereas SILYK1 and SILYK13 mediate chitin-triggered defense responses [59]. Ectopic over-expression of *SILYK13* was reported to cause more severe cell death in *N. benthamiana* leaves, which was not visible in the case of *SILYK1* over-expression [59], implying a distinct function of these receptors. A recent report described that SILYK4 has binding affinity to chitin, and following chitin detection, SILYK4-SILYK1 complex formation was induced in a SILYK4-dependent manner [60]. It was also observed that over-expression of *SILYK4* improved resistance in both the leaves and fruits of tomato against *B. cinerea* [60]. Following chitin detection, SILYK1 interacted with TPK1b-related kinase1, a receptor-like cytoplasmic kinase (RLCK), and this interaction was necessary for chitin-induced immune responses and fungal resistance [77].

The interaction of those LysM-containing receptors, identified in non-model plants (Table 1), with common defense-associated co-receptors and downstream defense components following carbohydrate elicitor detection should, however, be elucidated further.

Table 2
Carbohydrate-induced defense responses and their potential to control biotic and abiotic stresses.

Carbohydrate elicitor	Carbohydrate source	Treatment received plant	Induced plant defense activities	Suppressed/ tolerated stress	Effect/s on the stress symptoms	Application mode	Concentration	Tested condition	Reference
Biotic Stresses									
Chitosan	<i>A. niger</i>	Rice	Enhanced antioxidant enzymes	<i>Xanthomonas oryzae pv. Oryzae</i>	Reduced lesion length and disease index reduction	Foliar spray	50 ppm	Field	[171]
Chitosan	Purchased	Tomato	Expressed defense genes <i>CEVI-1</i> , <i>NPR1</i> and <i>PALS</i>	<i>Cucumber mosaic virus</i>	No viral infection symptoms	Foliar spray	10 mL/plant	Greenhouse	[172]
Chitosan	Purchased	<i>Pinus pinaster</i>	Increased catalase, carotenoids, anthocyanins, phenolic compounds, and lignin contents	<i>Bursaphelenchus xylophilus</i>	Lower nematode populations in the induced plant	Mixed with plant substrates	80 mL per-plant	Growth chamber	[173]
Nano-sized chitosan	Purchased	Potato	Up-regulated <i>PR1</i> , <i>WRKY34</i> , and <i>PIK1</i>	<i>Phytophthora infestans</i>	Enhanced protection percentage (48.9 %)	Foliar spray	125 g/ha once per week	Field	[174]
Chitosan-thiadiazole-trifluorobutene	Purchased	Tomato	Improved chitinase and β -1,3-glucanase activity	<i>Meloidogyne incognita</i>	Kill the second juvenile; decrease the disease incidence	Dipping and root inoculation	1 mg/mL	<i>In vitro</i> and Greenhouse	[175]
COS-OGA	Purchased	Rice	Enhanced PAL activity	<i>M. graminicola</i>	Reduced number of galls and female nematodes	Foliar spray	62.5 ppm	Growth room	[176]
COS-OGA	Donated	Tomato	Up-regulated expression of <i>PR3</i> ; down-regulated SA-responsive genes	<i>Alternaria solani</i>	Reduced disease severity	Foliar spray	0.5 %	Growth room	[177]
Exopolysaccharide fructan	<i>Paenibacillus kribbensis</i> PS04	Tobacco	Elevated non-enzymatic and enzymatic antioxidants; decreased MDA content	<i>Rhizoctonia solana- cearum</i>	90 % control efficiency; lowered disease severity by more than 70 %	Foliar spray	6 g/L	<i>In vivo</i> (pots)	[178]
Alginate	<i>Bifurcaria bifurcata</i>	Date palm	Stimulated PAL activity and over-expressed SOD and LOX genes	<i>F. oxysporum</i>	Reduced mortality rate by up to 80 %	Soaking the roots	1 g/L	Greenhouse	[179]
Alginate oligosaccharide	Brown algae (Unspecified species)	Arabidopsis	ROS and NO burst; increased SA content; higher expression of resistance gene <i>PR1</i>	<i>Pseudomonas syringae pv. tomato</i>	Reduced degree of leaf wilting and yellowing area	Foliar spray	25 mg/L	Greenhouse	[180]
λ -carrageenan	<i>Acanthophora spicifera</i>	Rubber tree	Accumulated SA and scopoletin; <i>HbPR-1</i> and <i>HbGLU</i> genes expressed	<i>P. palmivora</i>	Lowered disease severity index	Foliar spray	0.5 mg/mL	Growth room	[181]
Ulvan	<i>Ulva fasciata</i>	Wheat	Enhanced β -1,3-endoglucanase and chitinase activity	<i>Zymoseptoria tritici</i>	Decreased disease severity by 45 %	Foliar spray	10 mg/mL	Greenhouse	[182]
Laminarin	Purchased	Grapevine	Not reported	<i>Erysiphe necator</i>	Reduced disease severity and incidence	Irrigation	90 g/ha	Field	[183]
OGAs	Polygalacturonic acid	Arabidopsis	Accumulated early signaling molecules and increased SA and JA hormones	<i>P. syringae pv. tomato</i> DC3000	Lower disease index; chlorotic and necrotic symptoms	Foliar Spray	25 mg/L	Phytotron	[184]
OGAs	Unspecified	Arabidopsis	Increased callose accumulation	<i>Myzus persicae</i>	Decreased the number of aphid offspring	Injection	200 μ g/mL	Controlled condition	[185]
OGAs	Sunflower plate pectin	Sugar beet	Enhanced expression of antioxidant enzyme genes: <i>GPX</i> and <i>SOD</i>	<i>R. solani</i>	Reduced the incidence of seedling damping-off	Seed drench	50 mg/L	<i>In vitro</i>	[186]

(continued on next page)

Table 2 (continued)

Carbohydrate elicitor	Carbohydrate source	Treatment received plant	Induced plant defense activities	Suppressed/ tolerated stress	Effect/s on the stress symptoms	Application mode	Concentration	Tested condition	Reference
Xyloglucan	Hemicellulose	Grapevine	Callose deposition; phytoalexin synthesis; PR proteins accumulation	<i>Botrytis cinerea</i>	Reduced lesion diameter by ~50 %	Foliar Spray	1 mg/mL	Greenhouse	[15]
Mannan oligosaccharides	Locust bean gum	Tobacco and rice	ROS and NO burst, stomatal closure, hypersensitive response, and PR-1a synthesis	<i>P. nicotianae</i> , <i>X. oryzae</i>	Reduced lesion lengths with 40 % control efficiency	Injection	200 mg/L	Growth chamber	[16]
LPS	<i>Xylella fastidiosa</i>	Grapevine	Expression of Class III peroxidase gene, protein kinases, and others	<i>X. fastidiosa</i>	Less internal tyloses and leaf scorch	Injection	50 µg/mL	Glasshouse	[95]
Fructan oligosaccharides	Microbial and plants	Arabidopsis, Chicory, and Rocket	Increased ROS burst and apoplastic sugar content	<i>B. cinerea</i>	Reduced lesion size	Leaves spray	5 g/L	Growth chamber	[187,188, 189]
Fructan (levan)	<i>Dactylis glomerata</i>	Apple	Enhanced soluble sugars content	<i>Venturia inaequalis</i>	Decreased pathogen sporulations; directly limit pathogen growth	Leaves spray	1 g/L	Controlled greenhouse	[190]
Fructan (Inulin)	Chicory	Lettuce	Accumulation of H ₂ O ₂	<i>B. cinerea</i>	Decreased diseases symptoms	Leaves spray	5 g/L	Growth chamber	[191]
Oligo-Mix (CEOS, XOS, COS)	Cotton linters, crab and shrimp shells, and corn cob	Tomato	Up-regulation of genes for pathogenesis-related proteins, ethylene production, and cell wall synthesis	<i>Oidium</i> spp.	Significantly reduced the disease symptoms	Leaves spray	20 mg/mL CEOS, 40 mg/mL XOS and 20 mg/mL COS	Greenhouse	[192]
Abiotic Stresses									
Chitin	Unspecified	Arabidopsis	Decreased excessive H ₂ O ₂ ; over-expression of heat tolerance gene, <i>ERECTA</i>	Heat	Improved germination parameters and hypocotyl length	Seed priming	20 mg/L	<i>In vitro</i>	[50]
Chitosan	Purchased	Maize	Elevated enzymatic antioxidants activities; alternative oxidase synthesis; increased respiration rate	Salinity	Greater root length and plant height as compared to control	Foliar spray	0.1 % w/v	Growth chamber	[193]
Chitosan	Unspecified	Lettuce	Enhanced antioxidants, chlorophyll <i>a</i> , and K ⁺ accumulation; reduced membrane lipid peroxidation	Salinity	Enhanced total leaf area, shoot fresh weight, and shoot and root dry weight	Foliar spray	100 mg/L	Cultivation room	[194]
Chitosan	Unspecified	Rice	Elevated antioxidants; enhanced Chlorophyll <i>a</i> , <i>b</i> , and carotenoids	Drought	Improved shoot fresh and dry weight	Seed drench then foliar spray	40 mg/L	Greenhouse	[153]
Chitosan	Unspecified	Sorghum	Increased antioxidants, photosynthetic rate, total proteins and total amino acids contents	Drought	Higher production of panicle and grain dry biomass; 57 % enhanced drought tolerance	Foliar spray	80 mg/L	Greenhouse	[195]
COS	Shrimp and crab shell	Rice	Increased proline and glutamate content for osmo-regulation	Cold	Increased fresh weights of shoots and roots	With growth medium	150 mg/L	Growth chamber	[196]
Chitosan nanoparticles	Prepared from commercial chitosan	<i>Salvia abrotanoides</i>	Improved relative water content, total chlorophyll, secondary metabolites, antioxidant enzymes	Drought	Increased stomatal density and decreased stomatal aperture size	Foliar spray	60 and 90 ppm	Greenhouse	[197]

(continued on next page)

Table 2 (continued)

Carbohydrate elicitor	Carbohydrate source	Treatment received plant	Induced plant defense activities	Suppressed/ tolerated stress	Effect/s on the stress symptoms	Application mode	Concentration	Tested condition	Reference
Trehalose	Unspecified	<i>Paeonia lactiflora</i>	Decreased ROS and MDA accumulation; increased antioxidant enzymes	High temperature	Reduced stomatal closure	Foliar spray	300 mM	Growth chamber	[198]
Trehalose	Unspecified	Quinoa	Decreased H ₂ O ₂ and MDA accumulation; increased antioxidant enzymes activity; enhanced osmoregulators	Drought	Improved drought tolerance	Foliar spray	0.5 mM	Field	[199]
Trehalose	Unspecified	Tomato	Elevated antioxidant enzyme activities; eliminated MDA content; maintain ion hemostasis	Salinity	Promoted the growth and biomass of tomato seedlings	Foliar spray	10 mM	Greenhouse	[200]
Trehalose	Unspecified	Rice	Enhanced net photosynthetic rate and osmoregulators	Salinity	Increased vegetative parameters and all yield attributes	Foliar spray	25 × 10 ⁻³ mg	Field	[201]
Sucrose	Unspecified	Arabidopsis	Accumulation of polyamines	Atrazine (herbicide)	Increased primary root length and fresh weight	With growth medium	80 mM	<i>In vitro</i>	[202]
Polysaccharide	<i>Lessonia nigrescens</i>	Wheat	Decreased membrane lipid peroxidation; increased chlorophyll content and antioxidant activities; regulated intracellular ions	Salinity	Increased root and shoot length by 12 % and 37.3 % respectively	Unspecified	Unspecified	Growth incubator	[203]
Xyloglucan oligosaccharides	Unspecified	Ramie	Increased chlorophyll and carotene content of leaves; reduced levels of H ₂ O ₂ , MDA, and proline; improved antioxidant enzymes activity; reduced transfer of cadmium to the shoot	Cadmium toxicity	Increased root and shoot length by 19.15 % and 23.16 % respectively; enhanced fresh weights of roots, stems, and leaves	Mixed with growth solution	20 µg/L	Growth room	[204]

APX, ascorbate peroxidase; CAT, catalase; CEOS, cellulose oligosaccharide; COS, chitin/chitosan oligosaccharides; GLU, glucanase; GPX, glutathione peroxidase; JA, jasmonic acid; LOX, lipoxygenase; LPS, lipopolysaccharide; MDA, malondialdehyde; NPR, non-expresser protein receptor; OGA, oligogalacturonide; PAL, phenylalanine ammonia lyase; PPO, polyphenolperoxidase; PO, peroxidase; PR, pathogenesis-related; ROS, reactive oxygen species; SA, salicylic acid; SOD, superoxide dismutase; XOS, xylo-oligosaccharide.

2.2. Malectin/malectin-like receptors

Plant malectin/malectin-like receptor kinases containing a malectin-like domain in their ECD are commonly known for their role in arrays of biological activities such as reproduction, growth, hormonal responses, immunity, and sensing cell wall integrity [78]. Malectin ECD of these PRRs appears in association with LRR domains in their extracellular moiety [79]. Plant cell walls, composed of mainly cellulose, hemicellulose, and pectin, are perturbed when plants are exposed to biotic and abiotic stresses that could modify or destroy the structure of these carbohydrates [80]. The malectin-containing receptors in plants are capable of sensing cell wall perturbation and detecting fragments of these cell wall carbohydrates, which is crucial in maintaining cell wall integrity and plant immune responses activation [78].

The impaired oomycete susceptibility 1 (IOS1), which is a member of LRR-malectin-like RLK, was associated with CERK1 and was required for chitin-induced PTI in Arabidopsis [81]. The extracellular region of FERONIA (FER), a group of *Catharanthus roseus* receptor-like kinase 1-like (CrRLK1L) with malectin-like ECD, has been shown to interact with pectin and its fragments [82,83]. Salinity-induced impairment of the cell wall activates FER-dependent Ca^{2+} signaling to control the burst of root cells under salt stress [82]. Loss of function of FER blocked PR expression, cell wall remodeling, and the release of elicitor-active pectic polysaccharides in salt-stressed and lignin-modified plants [82,84]. FER also plays key roles in multiple biological processes, such as plant growth and flowering, and modulates defense responses by promoting receptor and co-receptor complex formation [85,86].

Another RLK that contains LRR-malectin is celooligomer-receptor kinase1 (CORK1), which is identified as the celotriose receptor and is necessary for celotriose-triggered Ca^{2+} influx, ROS production, MAPKs activation, and maintaining cell wall immunity in Arabidopsis [71]. Martín-Dacal et al. [72] recently found that CORK1 showed high affinity to both celotriose and cellopentose, further supporting its role in cello-oligomer perception. The celotriose-activated CORK1 pathway is involved in the phosphorylation of several proteins required for cellulose biosynthesis [87]. Phosphorylation of those assisting protein trafficking from the Golgi apparatus to the plasma membrane was an early target of celotriose signaling in Arabidopsis, indicating that celotriose primarily induces cellulose biosynthesis [87]. Martín-Dacal et al. [72] demonstrated that two LRR-malectin-containing RLKs, closely related to CORK1, are involved in triggering cytoplasmic Ca^{2+} elevation by MLGs. However, MLGs are unable to bind to the CORK1 [72]. Importantly, PTI induced by MLGs in Arabidopsis was partly reliant on CERK1, LYK4, and LYK5 [19,72]. Nevertheless, the specific recognition mechanism for MLGs has not yet been well understood. Martín-Dacal et al. [72] suggested that a LRR-malectin-containing RLK (*impaired in glucan perception4*, *IGP4*) might function as a co-receptor in the receptor complex for both celooligomers and MLGs and downstream immune response initiation in Arabidopsis.

2.3. Lectin/lectin-like receptors

Lectin-RLKs are among the RLK subfamilies and are characterized by a lectin domain located in their extracellular region [88]. Based on the N-terminal lectin domain variability, lectin-RLKs are classified as G-type (*Galanthus nivalis* agglutinin-related lectin domain), C-type (calcium-dependent), and L-type (legume-like) [88]. Lectin-RLKs have been reported to play a key role in regulating plant defense responses against biotic and abiotic stresses [88]. In plants, receptors with a lectin domain are able to detect carbohydrate-containing PAMPs/DAMPs (e.g., OGAs, PGN, and LPS) derived from pathogens or damaged plants during infection [89].

The lipo-oligosaccharide-specific reduced elicitation (LORE) receptor, a G-type lectin RLK, was initially reported to be required for the LPS-induced immunity of Arabidopsis [90]. Afterwards, Kutschera et al. [91] showed that LORE did not directly detect LPS but was rather specifically bound to medium-chain 3-hydroxy fatty acids existing in the lipid-A part of LPS. Thus, in Arabidopsis, LORE is not a receptor for LPS. Importantly, the core oligosaccharide and O-chain of LPS are involved in detection by the RLKs in a multi-protein complex [92]. For the perception of hexaacylated LPS, derived from *Escherichia coli*, the G-type lectin S-receptor kinase and brassinosteroid-insensitive 1-associated receptor kinase 1 (BAK1) are among the identified RLKs in Arabidopsis [93]. Hussan et al. [92] identified three G-type lectin S-receptor kinases, i.e., SD1-1, SD1-13, and At1g6752, as receptors of LPS in Arabidopsis. The first two detect LPS derived from *Pseudomonas syringae*, while the third senses LPS purified from *Xanthomonas campestris* [92]. The elicitation activity of three LPS obtained from *P. syringae*, *X. campestris*, and *Burkholderia cepacia* resulted in chemically different changes to the metabolome of Arabidopsis [94]. These LPS showed structurally distinct features mainly in their O-chain and lipid-A regions, indicating different possible recognition mechanism(s) in Arabidopsis [94]. Desaki et al. [37] described that a distinct receptor, OsCERK1, was required as a receptor/co-receptor for LPS detection and induced immune responses in rice but not in Arabidopsis. Furthermore, grapevine primed with LPS obtained from *Xylella fastidiosa* showed differential expression of receptor kinases, including two LRR-RLKs and two wall-associated kinases (WAKs), which might be involved in the detection of LPS [95]. Thus, the LPS recognition mechanism (s) in plants is/are significantly different depending on the LPS chemotypes and plant species.

Rice genes encoding cell surface-localized G-type receptors, i.e., OsLecRK1, OsLecRK2, and OsLecRK3, have been reported to confer broad-spectrum resistance against rice-feeding pests [96]. Upon brown planthoppers feeding on rice, *Poaceae*-specific MLG, β -1,3/1,4-D-glucan, production was significantly increased, leading to enhanced resistance to the pest through improved cell wall thickness and modulating OsLecRK1-mediated defense signaling [75]. Interestingly, the MLG-derived oligosaccharides bind to OsLecRK1 and regulate its activity during rice-brown planthopper interactions [75]. On the other hand, MLG-derived oligosaccharides released from the rice cell wall during *Magnaporthe oryzae* infection are detected by OsCERK1 and trigger defense signaling [18]. Thus, it will be interesting to understand the interaction of these two receptors in detecting MLG-derived oligosaccharides.

2.4. WAK receptors

Wall-associated kinases (WAKs), a subset of the RLK family, are characterized by the presence of epidermal growth factor domains in their ECD [97]. They play a critical role, including in plant responses to biotic and abiotic stresses. WAKs are potential candidate receptors/co-receptors of carbohydrates released during plant-pathogen interactions [97].

Arabidopsis WAK 1 (AtWAK1) and AtWAK2 are known to detect pectin, pectin fragments, and OGAs and mediate resistance to various pathogens [30]. Importantly, cell wall-extracted elicitors rich in pectin derivatives induce PR genes expression in *wak1/2* double mutant Arabidopsis [84]. Likewise, these elicitors failed to trigger *PR1*, *PR2*, and *PR5* expression in *wak1/2/3/4/5* quintuple mutant lines [84], showing that all five WAKs in Arabidopsis might function redundantly in detecting pectin-derived elicitors. OGA-treated Arabidopsis plant showed an elevated Ca^{2+} influx, ROS generation, MAPK3/6 activation, and expression level of defense genes [98–100]. According to Kohorn et al. [101], deletion of the WAK gene did not change the transcriptional response induced by OGAs, only the formation of ROS. Wheat treatment with pectin enhanced the transcript level of *TaWAK-6D*, a WAK-encoding gene located on chromosome 6D, suggesting that it might participate in pectin-induced immunity in the plant [102]. Similarly, *TaWAK7D*, which was required for resistance to *Rhizoctonia cerealis* infection, was found to be involved in pectin-mediated defense responses in wheat [103].

WAKs are also involved in chitin-induced defense responses in plants. For example, Delteil et al. [104] found that CEBiP partially modulates the expressional regulation of rice WAK genes following chitin treatment. The cotton GhWAK7A, which can't bind to chitin directly, participated in chitin-triggered defense responses to control fungal infection via promoting dimerization and phosphorylation of the chitin receptor complex, i.e., GhLYK5-GhCERK1 [58]. The expression levels of *GhMAPK3* and *GhMAPK6* were found to be lower in *GhWAK7A*-silenced plants than in control plants following chitin treatment [58]. Similarly, silencing of *TaWAK2A-800* compromised wheat resistance against fungal diseases and reduced the expression level of chitin-responsive defense genes, including *TaCERK1*, *TaRLCK1B*, and *TaMAPK3* [105]. *TaWAK7D* was involved in chitin-mediated expression of defensive genes [103]. However, the wheat CEBiP has direct chitin-binding activity, and its dimerization with TaCERK1 was required for chitin-signaling [70]. Considering the fact that the *TaWAK2A-800* and *TaWAK7D* are involved in chitin-induced defense responses and the important roles TaCEBiP and TaCERK1 played in wheat chitin-signaling, the potential relationship of these WAKs with the TaCEBiP and TaCERK1 needs to be investigated further.

Plant WAK-like (WAKL) proteins, membrane proteins containing ECD structurally similar to WAKs, are associated with pectin sensing in plants. Huerta et al. [106] reported that resistance to *Fusarium oxysporum* 1 (RFO1), a WAKL-protein in Arabidopsis, was vital for resistance against *Fusarium oxysporum* via detecting alterations in the pectin methylation. The RFO1 ECD bonded to demethylated pectin *in vitro* [106], just as observed in AtWAK2 [107]. In response to *F. oxysporum*-induced variations in pectin methylation, RFO1 controls the expression of specific defensive genes by regulating the phosphorylation status of MAPK3 and MAPK6 [106].

2.5. Role of co-receptors in carbohydrate signaling

Most commonly, PRRs cooperate with co-receptors to initiate downstream defense activities. Mostly the co-receptors BAK1 and its orthologue, BAK1-Like Kinase 1 (BKK1), function with non-carbohydrate ligand receptors such as EFR, PEPRs, and FLS2 [30]. In some studies, these co-receptors engage with carbohydrate-ligand receptors. For example, BAK1 mediates the phosphorylation of the juxtamembrane (JM) domain of CERK1, which is important for signaling in response to chitin recognition [108]. OGA-induced immunity in Arabidopsis was impaired by the lack of *BAK1* and *BKK1* [109], implying that both BAK1 and BKK1 are important in chitin and OGA signaling in Arabidopsis. On the other hand, Johnson et al. [110] observed that celotriose-induced calcium enhancement in Arabidopsis was BAK1-independent. Likewise, it was confirmed that BAK1 was not required in cellobiose recognition and subsequent signaling, as no change in expression of TF was observed in *bak1-5* mutated Arabidopsis after cellobiose elicitation [111]. Furthermore, BAK1 was not involved in the recognition of β -1,3/1,4-MLG oligosaccharides in barley and Arabidopsis [112].

3. Signal transduction downstream of PRRs-Carbohydrate complex

Ligand sensing by ECD activates autophosphorylation of the PRR's cytoplasmic domain, vital for signal transduction. Chitin was observed to rapidly induce *in vivo* phosphorylation of AtCERK1 at multiple residues in the JM and kinase domains [113]. Threonine and tyrosine residues in the kinase domain are key autophosphorylation sites of AtCERK1 [114,115]. Besides, the JM domain was required for autophosphorylation of AtCERK1 and OsCERK1 and played a conserved role in the chitin-induced signaling pathway [116]. Following receptor/co-receptor phosphorylation and activation, multiple downstream defense components such as Ca^{2+} channels, NADPH oxidases, RLCKs, heterotrimeric G-proteins, ubiquitin ligases, MAPKs, phytohormones, and TFs are activated, all of which are crucial for plant stress resistance/tolerance development [13,89].

3.1. RLCKs transduce carbohydrate-triggered signaling

PRRs dynamically interact with RLCKs, which is necessary for linking an activated PRR with multiple defense signaling components [26]. In response to chitin perception, OsRLCK185 directly interacted with and phosphorylated OsCERK1, which in turn caused OsMAPK3 and OsMAPK6 activation to induce MAPK cascade signaling in rice [117]. Later, the work of Wang et al. [118] showed that OsRLCK185 also interacted with OsMAPKKKε and increased chitin-induced MAPK3/6 activation in rice. Besides, OsRLCK185 interacted with and phosphorylated a Ca^{2+} channel, cyclic nucleotide-gated channel 9 (OsCNGC9), to control chitin-triggered Ca^{2+} influx

[119]. Other RLCK-II members, including OsRLCK57, OsRLCK107, OsRLCK118, and OsRLCK176, were reported to interact with OsCERK1 and mediate the chitin- and PGN-induced ROS generation in rice [120]. Downstream of SDS2 (monocot RLK SPL11 cell death suppressor 2), OsRLCK118 and OsRLCK176 interacted with and phosphorylated the NADPH oxidase OsRbohB to initiate ROS generation and programmed cell death during fungal infection [121]. Importantly, OsRLCK118 participates in rice immunity by regulating salicylic acid (SA)- and jasmonic acid (JA)-mediated expression of PR genes because SA and JA treatment improved *OsRLCK118* expression while the expression of PR genes was impaired in *osrlck118* mutants [122].

In addition, broad-spectrum resistance 1 (BSR1; OsRLCK278), a member of the rice RLCK-VII subfamily, has mediated chitin-, PGN-, and LPS-elicited disease resistance in rice [123,124]. In response to these PAMPs, over-expression of *BSR1* in rice has enhanced H₂O₂ generation and defense-associated genes expression in suspension-cultured cells and leaf strips [124]. The work of Sugano et al. [125] demonstrated that BSR1 has kinase activity and that both tyrosine and serine/threonine were essential for its activation, implying that it may mediate phosphorylation signaling downstream of PRRs. Kanda et al. [126] recently described that overexpressed BSR1-mediated defense response enhancement was dependent on PAMP-induced OsCERK1 activation. Furthermore, rice brassinosteroid-signaling kinase 1–2 (OsBSK1-2), another subfamily of RLCK-II, was reported to participate in chitin signaling, where silencing of *OsBSK1-2* impaired expression of PR genes in response to chitin treatment and plant resistance to fungal infection [127]. Nevertheless, how OsBSK1-2 transduces signals from the chitin receptor complex to trigger downstream defense responses is poorly understood.

In Arabidopsis, PBL27 (an orthologue of OsRLCK185) interacted with AtCERK1 via phosphorylation and regulated chitin-induced downstream signaling [128,129]. It links the chitin receptor complex and the intracellular MAPK cascade via activation of MAPK kinase kinase 5 (MAPKKK5) [43]. The PBL27 also interacted with the slow-type anion channel (SLAH3) to mediate chitin-induced stomatal closure and anti-fungal immune responses [130]. Moreover, Desaki et al. [131] recently reported that PBL27 interacted with and was phosphorylated by calcium-dependent protein kinases (CPK)-related protein kinases (CRK2) in response to herbivore-secreted polysaccharide elicitors. This CRK2-PBL27 interaction was primarily responsible for the polysaccharide elicitor-induced transcription of *PDF1.2* in attacked plants [131]. Rather than PBL27, RLCK II-4 members, including PBL19 and PBL20, were involved in mediating the chitin-induced ROS production and MAPK activation [132]. Most importantly, PBL19 directly phosphorylated MAPKKK5, which was required for chitin-induced MPK3/6 activation [133]. Besides, after activation by chitin, PBL19 fractions moved into the nucleus, inducing transcriptional self-amplification via WRKY8 and enhanced disease susceptibility (EDS1)-dependent constitutive defense responses, which improved fungal resistance [134].

Other regulatory proteins, in addition to the RLCKs, are involved in the carbohydrate-activated receptors linking with downstream signaling pathways. For example, Yamaguchi et al. [135] identified OsDRE2, an iron-sulfur cofactor, as an interactor of OsRLCK185 that positively regulated chitin-induced immune responses. Similarly, heterotrimeric G-proteins could physically interact with defense-related receptors to transduce extracellular ligands such as chitin and flg22 [136]. OsRac1, one of the rice Rac/Rop small GTPases, was phosphorylated by the cytoplasmic domain of OsCERK1, which in turn up-regulated ROS production in rice after chitin perception [137]. Recently, Zhao et al. [138] showed that rice extra-large G3 (OsXLG3), a subfamily of G α proteins, participated in both early and late immune responses, whereas OsXLG2 appeared to be involved in late immune responses following chitin detection. Both OsXLG2 and OsXLG3 were able to physically associate with the OsCERK1-OsRLCK185-OsRLCK176 receptor complex [138]. Arabidopsis triple mutant lines in *xlg1/2/3* showed reduced chitin-induced activation of MAPK cascades and resistance to pathogen infection, indicating that they all function redundantly [139]. These three XLGs interacted with MAPK cascades, including MAPKKK3/5, MPKK4/5, and MPK3/6, which are commonly involved in chitin signaling [139]. Likewise, Arabidopsis mutants in *Atran1* (a gene decoding into a small G-protein, ATRAN1) showed reduced chitin-triggered accumulation of ROS and NO and impaired stomatal closure [140]. The role of G-proteins in mediating chitin-induced immunity was also observed in other plant species. For example, the XLG proteins of tobacco, *Nicotiana benthamiana*, interacted with the NbCERK1 receptor in a luciferase complementation image assay [141], and *N. benthamiana* mutants in XLG proteins showed significantly reduced chitin-induced ROS burst and resistance to fungal infection [141]. GhGPA (a member of the G α protein subunit) enhanced resistance to fungal infection in cotton through the induction of ROS generation and activation of SA and JA signaling pathways [142].

Plant U-box-type (PUB) ubiquitin ligases are additional components involved in the positive regulation of chitin-mediated plant immunity. Desaki et al. [29] identified a CERK1-interacting E3 ubiquitin ligase, PUB4, which positively regulated ROS generation for chitin signaling in Arabidopsis. PUB4 interacted with AtCERK1 via phosphorylation [129] and was involved in chitin-induced immune responses [29]. Recently, it was demonstrated that PUB4 physically interacts with PBL27 [143], indicating that PBL27 also plays an important role in the PUB4-AtCERK1 complex. The C-terminal region (ARM repeats), not the E3 ligase activity, of PUB4 was required for its function in chitin-triggered immunity in Arabidopsis [143]. In addition to PUB4, PUB2 was found to mediate chitin-induced ROS generation and callose accumulation but not MAPK activation in Arabidopsis [143]. Unlike PUB4, PUB2 was unable to interact with AtCERK1 and PBL27 [143]. On the other hand, both PUB2 and PUB4 were able to physically associate with XLGs, which are mostly localized in the plasma membrane [144]. In rice, silencing of *PUB44* led to impaired chitin- and PGN-triggered defense activities and plant resistance to *Xoo*, implying that *PUB44* plays an important role downstream of OsCERK1 [145]. *PUB44* participated in chitin-triggered TF activation via inducing degradation of the PBI1 (*PUB44-INTERACTING 1*) protein, which can interact with WRKY45 and negatively regulate its activity [146].

3.2. Early-acting signaling events mediate carbohydrate-induced immunity

The induction of PRRs/RLCKs activities also promotes activation of early defense signaling components such as Ca²⁺ channels, NADPH oxidase respiratory burst oxidase protein D (RBOHD), and MAPKs [147]. These early signaling events participate in

carbohydrate elicitor-induced plant immunity by connecting cell membrane responses to nuclear transcriptional reprogramming, which leads to regulate defense-related gene expression [13] (Fig. 1).

Extracellular signal activating Ca^{2+} influx is one of the early cellular responses that act as a secondary messenger involved in numerous plant defense responses signaling [147]. Chitin-induced activation of Botrytis-induced kinase 1 (BIK1) in Arabidopsis led to phosphorylation and activation of Ca^{2+} channels (CNGC2 and CNGC4), and this caused enhanced cytosolic Ca^{2+} concentration [148]. It has been reported that extracellular Ca^{2+} influx participated in cascading the OGA-induced resistance in soybean cells [149] and in tomato fruits [100]. Similarly, MLG oligosaccharides activated the influx of Ca^{2+} in Arabidopsis [19]. The work of de Azevedo Souza et al. [111] demonstrated that cellobiose-induced Ca^{2+} signaling cascades led to the expression of the defense-related TF gene (*WRKY30*) in Arabidopsis. Polysaccharide peptide- and OGA-induced Ca^{2+} influx subsequently increased H_2O_2 and SA content [150] and activated MAPK cascade [151], respectively, showing that they are able to activate complex interactions in the signaling network. Besides, activation of calmodulin, calcium-dependent protein kinases (CPK), and plasma membrane cation binding protein 1 (PCaP1), which can detect Ca^{2+} to activate defense-related TFs and defense responses, was increased in response to OGAs [99,151,152] and chitosan treatments [153]. In Arabidopsis, AtCPK5 has phosphorylated AtLYK5 and regulated chitin-induced MAPK3/6 phosphorylation, defense-related gene expression, and callose deposition [154]. PCaP1 interacted with Ca^{2+} and Ca^{2+} -calmodulin complexes to activate plant defense responses [155]. Calmodulin participated in ROS generation through plasma membrane-localized RBOHD activation [157]. CPK and Ca^{2+} direct binding play an important role in ROS generation through plasma membrane-localized RBOHD activation [157]. The CPK5 has linked Ca^{2+} -signaling with N-hydroxy-L-pipecolic acid- and SA-signaling-dependent immunity [158]. In addition, calmodulin and calmodulin-like proteins decode Ca^{2+} signals to calmodulin-binding TFs to activate immune-related genes expression [159].

In plants, activated receptor-triggered ROS generation is considered as signaling molecule with vital roles in hypersensitive response, stomatal closure, callose accumulation, and cell wall reinforcement [147]. Besides, it interacts with defense hormonal signaling pathways and TFs [160,161]. Carbohydrate elicitors are effective in inducing ROS generation in diverse stressed plant species (Table 2) and (Fig. 1). Mostly, the oxidative burst occurring within 30 min after carbohydrate elicitor treatment is rapid and transient [38,162,163], implying that the oxidative burst necessitates activation of pre-existing enzymes. In addition, the carbohydrate- and oligomer-induced ROS generation is dose-dependent [18,164–166], and the optimum concentration depends on the type of carbohydrate elicitor and the plant species being treated. The oxidative burst triggered by receptor-mediated carbohydrate perception was induced by membrane-localized NADPH oxidases, e.g., RBOHD [72,167,168]. Usually, the RBOHD is linked with multiple PRR complexes even before activation. For activation, RBOHD was directly phosphorylated by BIK1 after PRR was triggered by PAMP to induce ROS burst [169]. The activity of RBOHD was required for the special accumulation of SA [170].

Similar to Ca^{2+} - and ROS-signaling, PRRs and RLCKs trigger MAPK activation, which is key to many plant defense responses. A typical MAPK cascade follows sequentially activated protein kinases: first, membrane-bound MAPKKK proteins phosphorylate MAPKK proteins, which in turn phosphorylate MAPK proteins [24]. MAPKKK and MAPKK signaling cascades triggered by various carbohydrate elicitors, for example, mannan oligosaccharides, cellodextrins, OGA, and MLG, have been shown to induce MAPK3/6 phosphorylation [16–19,99]. In rice, OsMAPKKKε interacted with OsMAPKK4 and then phosphorylated it, which is essential to cascading chitin-induced signaling into MAPK3/6 [118]. In Arabidopsis, MAPKKK3/4/5 acts upstream of MAPK4/5-MAPK3/6 to regulate chitin-induced immunity [205]. The work of de Azevedo Souza et al. [111] demonstrated that cellobiose-induced expression of *WRKY30* was reduced 20-fold in the *mpk6-2* mutant, implying MAPK6 has a key role in signal cascading from the cytosol to the nucleus. Likewise, chitin-triggered MAPK activation was required for *WRKY45* activation in rice [146].

3.3. Phytohormones regulate the carbohydrate-triggered defense signaling

Phytohormones, including SA, JA, ethylene (ET), abscisic acid (ABA), brassinosteroid (BR), and gibberellic acid (GA), play indispensable roles in the regulation of plant defense responses. SA- and JA/ET-signaling pathways are considered to be central for plant defense responses, whereas ABA, BR, and GA are believed to be involved in plant defense by controlling the SA- and JA/ET-signaling pathways [206]. Recognition of PAMP, DAMP, or elicitor activates hormonal signaling pathways and leads to gene expression alteration, causing specific defense response elicitation. Generally, the SA pathway is required to resist biotrophic and hemibiotrophic pathogens, whereas the ET/JA pathway is important to trigger resistance against necrotrophic pathogens and herbivore insects [207]. The chitosan oligomer that caused disease resistance in tobacco was found to be primarily SA-, rather than JA-, pathway-dependent [208]. In contrast, chitosan treatment of tobacco primed the accumulation of JA and its conjugate JA-isoleucine, but no impacts were observed on SA and ABA [209]. With regard to the chitosan oligomer-OGA (COS-OGA) effect on hormone signaling, the SA-responding genes were strongly up-regulated, while the JA/ET signaling marker genes remained constant in COS-OGA-treated tomato seedlings to control *Leveillula taurica* [210]. In contrast, van Aubel et al. [211] showed that the treatment of COS-OGA effectively protects potato leaves from *Phytophthora infestans* infections by controlling SA pathway activation. Similarly, COS-OGA strongly up-regulated the JA responsive gene expression but down-regulated the SA-signaling marker gene expression in tomato to control *Alternaria solani* [177].

Each phytohormone activates a specific molecular pathway, and their signaling pathways can crosstalk antagonistically or synergistically [207]. The crossroad between these hormones is the non-expressor of pathogenesis-related protein 1 (NPR1), which is categorized as a SA receptor [212,213]. Upon accumulation of SA, the NPR1 oligomers are converted to monomers by thioredoxins, then the monomers enter the nucleus, and together with TFs, NPR1 induce SA-responsive genes expression [206]. NPR1 is also involved in SA-mediated suppression of the JA pathway to assist when plants prefer SA over JA [207]. However, in the presence of high ET, NPR1 is no longer needed for SA/JA antagonistic crosstalk [207].

JA and its active derivative form, jasmonoyl-isoleucine, are lipid-derived hormonal molecules that regulate plant defense responses. Upon JA accumulation, the jasmonoyl-isoleucine is recognized by a coronatine-insensitive 1 receptor protein, leading to jasmonate zim (JAZ) repressor degradation, which subsequently activates the expression of JA-responsive genes [206]. Induction of the JA/ET pathway has a cooperative effect on JAZ and ethylene TFs, which is important for SA pathway repression [207].

Claverie et al. [15] found that xyloglucan-elicited disease resistance in grapevine and Arabidopsis cell suspensions was SA, JA, and ET pathway-dependent. Chitosan application to pea plants, on the other hand, resulted in the activation of both SA- and JA-mediated defense responses [214], indicating that both SA- and JA-pathways are involved in synergistic ways to modulate these carbohydrates' elicited immune response.

3.4. Transcription factors can be activated by carbohydrate elicitors

Transcription factors (TFs) are regulators of gene expression and are involved in various biological processes. Many TFs, including AP2/ERF, bZIP, MYB, and WRKY, are known to play vital roles in transcriptional reprogramming during plant-microbe interactions [89]. Carbohydrates can also act as an inducer of plant defense responses by triggering the activation of TFs involved in defense-related gene expression and hormonal signaling. For example, in tomato, chitosan application primed the up-regulation of MYB20 and WRKY51/72 [209], which are involved in cell wall formation [215] and SA-mediated JA-pathway suppression [216,217], respectively. Likewise, laminarin treatment of monocots and dicots induced expression of *HvWRKY1* and *HvWRKY2* [38]. In another study, the application of chitosan induced B3 family TF expression in drought-stressed rice [153]. Conversely, AP2/ERF and some WRKY TFs genes expression were repressed in response to saccharin, chitosan, and COS-OGAs application to plants [209,177,218]. Some TFs are required for SA-mediated signaling, while others are involved in JA-mediated signaling [219].

3.5. Involvement of polyamines in carbohydrate-induced defense signaling

Beside those signaling molecules, polyamines have received attention due to their important signaling and regulation activities in stressed plants. The *Arginine Decarboxylase (ADC1)* and *ADC2* genes encoding enzymes involved in polyamine synthesis were differentially regulated in response to sucrose treatment [202]. Likewise, chitosan treatment elicited the accumulation of free and conjugated polyamines (putrescine, spermidine, and spermine) [220]. Furthermore, pre-treatment with exogenous spermine enhanced the concentration of endogenous sugars (glucose, fructose, and sucrose) in Arabidopsis seedlings after infection with *B. cinerea* [221]. The exogenous application of polyamines and sugars reduced the excessive accumulation of ROS via anti-oxidant enzymes activation [202, 221]. These findings indicated that the interplay between polyamine metabolism and sugar metabolism led to increased stress tolerance in plants. Various carbohydrate elicitors enhance amino acid content to alleviate stresses in plants (Table 2). On the other hand, Samari et al. [220] suggested that the biosynthesis of amino acids under stress conditions contributes to the homeostasis of polyamines. Thus, other than chitosan and sucrose, the effect of carbohydrate elicitors' application on polyamines metabolism in stressed plants needed investigation.

4. Carbohydrate-induced plant defense responses and their potential to control stresses

The carbohydrate-induced plant defense responses and their potential to control biotic and abiotic stresses have been discussed by several authors (Table 2 and Fig. 1). Those induced defense mechanisms mimic the stress-inducible natural defense mechanisms of plants. Notably, the intensity and consistency in increment of those induced defense-related metabolite levels and activities in the treated plants are variable according to the carbohydrate elicitor type, concentration, induced pathways, stress type, environmental factors, and treated plant type and developmental stage [209,171,222–224].

Generally, the plant resistance induction activities of carbohydrate elicitors are based on priming or eliciting effects. In the priming effect, carbohydrate elicitors initially trigger minor parts of a defense system that increase the plant's ability to defend itself against subsequent pathogen infection more rapidly or strongly. It is considered that priming provides an enhanced plant protection strategy without causing major metabolic and energy costs for the plant [187]. In elicitation activity, the plant defensive mechanisms are immediately activated upon application of the resistance inducer in the absence of infection.

Induced resistance in plants has many advantages in comparison to other forms of resistance. One of these is that it takes less time to initiate the defense response and the response is long-lasting [225]. The plant defense responses can be activated within a few minutes or days after carbohydrate elicitor application. For example, λ -carrageenan induced the expression of PR-genes and *13-lipoxygenase2* after a day of treatment [223]. Treatment with mixed-oligosaccharides of cellulose, xylose, and chitosan initiated MAPK3/6 phosphorylation and callose deposition within 20 min of application [192]. Once initiated, the induced defense response can be maintained for a certain period. For instance, chitosan-induced resistance in tomato and tobacco against *B. cinerea* was maintained for two weeks post-treatment [209]. Foliar application of COS-OGA induced resistance against *A. solani* that lasted for 28 days [177]. Treatment with laminarin and alginate resulted in induced date palm resistance to Bayoud disease for up to four and seven weeks, respectively [179]. Therefore, the induction mode, carbohydrate elicitor type, and plant species determine the time required to initiate the defense response and the durability of the induced resistance.

4.1. Biocidal activities of carbohydrate elicitors against phytopathogens/pests

The positive effect of exogenously applied carbohydrate elicitors to ameliorate plant stress is not only limited to improving plant defense systems but also has direct antimicrobial effects. Though the direct antimicrobial properties of carbohydrate elicitors *in planta* have been rarely reported, the strong biocidal activity of carbohydrates (e.g., chitosan) is due to the fact that they could form an impermeable polymer layer, leading to limited nutrient access to the pathogenic cell, which in turn caused starvation to death [27, 224]. Fluorinated-chitosan oligosaccharide derivatives were reported to have effectively killed the second instar larvae of *Meloidogyne incognita* [172], though Singh et al. [173] found no direct nematocidal activity in foliar applied COS-OGA. Gunupuru et al. [226], on the other hand, reported that *in vitro* treatment of chitosan, in combination with liquid seaweed extract or alone, significantly inhibited the mycelial growth of *F. graminearum*. Kappel et al. [224] similarly observed that chitosan has strong fungicidal activity, in which 60–100 % inhibition zone was recorded against tested *Fusarium* spp. In a similar study, it was also reported that an *in vitro* assay at 0.6 g/L chitosan concentration reduced the growth of *F. oxysporum* by 70 % [227]. Similarly, OGAs at 10 mg/L strongly inhibited the mycelial growth of *Rhizoctonia solani* in an *in vitro* experiment [186]. *In vitro* treatment of olive with alginate and ulvan effectively inhibited the mycelial growth of the *Verticillium dahlia*, a causative agent of verticillium wilt of olive [222]. Treatment with *Aspergillus niger* derived chitosan exhibited significant antibacterial activities against *Xoo* was increased with increasing treatment concentrations [171]. Laminarin-based formulated Vacciplant® also directly inhibited *Zymoseptoria tritici* conidial germination both *in vitro* and *in planta* [228]. On the other hand, ulvan showed no direct antifungal activity in both *in vitro* and *in planta* assays against *Z. tritici* [182].

4.2. Dependency of carbohydrate-induced immunity on environmental abiotic factors

The carbohydrate-induced plant defense responses and their potential to control stresses under field conditions have been discussed by a number of authors (Table 2). Under natural stress-plant interactions, plant defense responses are dependent on environmental factors such as light, relative humidity, temperature, and the circadian clock [229]. It has also been suggested that these environmental factors could limit the bioactivity of carbohydrate elicitors during field application [223]. Daytime-dependent defense responses were observed in tomato plants after chitosan treatment at night and in darkness [230]. While ET and O₂ were accumulated in tomato plants kept under light, their accumulation was inhibited in plants grown in darkness, indicating the light dependence of chitosan-induced local and systemic resistance development [231]. To the contrary, chitosan-induced NO generation was not light-dependent [231]. Various carbohydrate elicitors are potent in triggering plant immunity (Table 2); nevertheless, our knowledge is still limited about the dependency of carbohydrate elicitor-induced plant immunity on extrinsic factors.

5. Plants equilibrate chitosaccharides-induced immunity and symbiosis signaling

N-acetylglucosamine (N-GlcNAc)-containing molecules (COs) are also vital signaling factors when plants interact with beneficial microorganisms such as arbuscular mycorrhizal (AM) fungi and rhizobia bacteria to develop symbiotic relationships [232,233]. To induce symbiosis signals, rhizobia bacteria release an acetylated CO, lipochitooligosaccharides (LCO), commonly known as the Nod factor [234,235]. Recently, it has been recognized that LCO is a common component in the cell walls of a wide range of fungi [236]. AM fungi secrete Myc-factors, including LCOs and short-chain COs such as CO4 and CO5, to trigger symbiosis signals in the host plant [237–240]. It has been generally believed that CO- and LCO-induced symbiosis is limited to legumes. However, it was reported that non-legumes respond to these symbiosis signaling factors through calcium oscillations, indicating they are common features of both legumes and non-legumes [234,241,242]. Long-chain COs with degree of polymerization (DP) 6–8 are potent immunity elicitors [35, 42,243]. In contrast to this, CO8-activated symbiosis-related gene expression and calcium oscillation indicated that long-chain COs can elicit both immunity and symbiosis signaling [244,245].

In symbiosis, LysM-containing receptors such as nodulation factor receptor 1 (NFR1) and the NFR5 complex in *Lotus japonicas*, and LYK3-NFP (nodulation factor perception) complex in *Medicago truncatula* have been recognized as receptors of the LCOs [246–249]. It has been widely accepted that rhizobia and AM symbiosis share a common signaling pathway, and thus Nod-factors recognition may have evolved from Myc-factors receptors [250]. Indeed, the orthologue of NFP/NFR5 in tomato and *Parasponia andersonii* was required for AM symbiosis [251,252]. In contrast, the orthologue of NFP/NFR5 was not required for AM symbiosis [253]; rather, OsCERK1 (the orthologue of NFR1/LYK3) was involved in both chitin-induced defense responses and AM symbiosis signaling in rice [254,255]. Besides, CO-induced calcium oscillation was impaired in OsCERK-mutated rice in response to CO detection [239]. Likewise, it has been observed that CO receptors such as MtLYK3 and MtLYK9 in *M. truncatula*, PsLYK9 in pea, LjLYK12 in *L. japonicas*, and MaLYK1 in banana are involved in regulating both symbiosis and immunity signaling [54,63,251,256,257].

Interestingly, OsCERK1 was unable to detect CO4-5, suggesting that additional proteins other than CEBiP and NFR5, which can be associated with OsCERK1, are involved in symbiosis signal factor detection [253]. Similarly, PsLYR3, a co-receptor of PsLYK9, showed no binding ability to CO4-5, suggesting other co-receptors of PsLYK9 are required during the binding of these short-chain COs [55]. Besides, Feng et al. [245] demonstrated that combined treatment of both CO4-8 and LCO promoted symbiosis over immunity, indicating that there are additional proteins that function in this symbiosis. Thus, He et al. [244] recognized OsMYR1 (Myc factor receptor 1) as an OsCERK1 binding partner for the recognition of CO4 in rice to induce symbiosis signaling responses and AM colonization. It was also detected that recognition of CO4 suppressed the CO8-elicited ROS generation, which necessitated the CO4-binding receptor OsMYR1 [244,255]. Recently, Zhang et al. [258] found that in the presence of CO4, OsMYR1 competes with OsCEBiP to form an OsMYR1-OsCERK1 receptor complex, which inhibited immune induction and instead promoted symbiosis. However, in the absence of CO4, OsCERK1 was associated with OsCEBiP to cause downstream phosphorylation, which increased the sensitivity of rice to PAMP [258].

The bifunctionality of the same RLK has led to questions about how structurally related LysM receptor kinases induce specific response, symbiosis or immunity, in response to COs detection. Bozsoki et al. [62] observed that the ECD of chitin-binding receptors, LjLYS6/MtLYK9, in *L. japonicus* and *M. truncatula* were responsible for detection of long COs (DP 6–8) rather than CO4; pointed ECD are vital to discriminate symbiosis signal factors from immunity elicitors. Recently, Bozsoki et al. [259] reported that the LysM1 domain of NFR1 and CERK6 are critical in discriminating the selectivity for Nod-LCO and chitin detection. In the LysM1 domain of NFR1 and CERK6, Bozsoki et al. [259] identified four regions, and thereof, region one and two were critical for receptor functions in *planta*. They concluded that the ECD of NFR1 and CERK6 is a determinant for ligand detection and signaling specificity, which could be further modulated by their intracellular kinase domain. It was reported that YAQ, a conserved amino acid sequence at the intracellular kinase domain of NFR1 and orthologue, has an important role in shifting hosts from defense response to symbiosis [260]. Recently, Suzuki et al. [261] showed that the YAQ-containing region of NFR1 plays an important role in inducing symbiotic signaling through the establishment of NFR1-NFR5 receptor complex. Considering the existence of a wide range of fungi in the rhizosphere that contain mixtures of CO6-8, CO4-5, and LCO, further work is needed to clearly understand how a plant regulates signals induced by these ligands.

6. Structural features dependent bioactivity of carbohydrate elicitors

Carbohydrates have great potential to induce plant immunity and stimulate growth. However, they had distinctive bioactivity, and variation in structural characteristics is among the function-determining factors. Herein, we have described how the bioactivity of carbohydrates is influenced by their structural features.

6.1. Cellulose- and hemicellulose-derived oligosaccharides

Plant cell wall-derived oligosaccharides such as cellodextrins, xylans, xyloglucans, mannans, or MLG have been reported as DAMPs implicated in plant immunity elicitation [16,72,110,111,262–264]. Reported evidence shows that the plant defense elicitation activities of these cell wall-originating saccharide molecules are reliant on their degree of polymerization (DP). In grapevine, cellodextrin with DP 7 was the most active than those with DP 8 and 9 in eliciting H₂O₂ production [262]. Cellobiose (DP 2) was effective in eliciting Ca²⁺ influx, MAPK activation, *WRKY30* expression, and suberin biosynthesis in Arabidopsis [111]. Similarly, C1-oxidized cellobionic acid showed the highest defense-eliciting activity among cellodextrins with DP 2–4 [265]. However, cellotriose (DP 3) was the most active in eliciting *RBOHD*, *CYP81F2*, and *WRKY30* gene expression than cellodextrins with DP 4–6, while it was null in cellobiose-treated Arabidopsis plants [266]. With regard to hemicellulose-derived oligomers, Claverie et al. [15] reported that DP 7 heptamaloxyglucan mixed with a low concentration of higher DP 8–9 was effective in eliciting defense responses in Arabidopsis and grapevine. In another study, wheat hemicellulose-derived pentose arabinoxytan with DP 3–5 triggered an intense Ca²⁺ burst in treated Arabidopsis plants, while it was reduced in DP 2 treated groups [17]. This was confirmed by that acid-hydrolyzed pentasaccharides 3³- α -L-arabinofuranosyl-xylotetraose lost their activity in inducing Ca²⁺ burst [17]. In Arabidopsis, the strongest eliciting activity was recorded from xylotetraose (DP 4), followed by xylotriose (DP 3), while xylo-oligosaccharides with DP 5 and DP 2 showed reduced activity [192]. Furthermore, Escudero et al. [264] showed that modification of the degree of xylan acetylation in plant cell walls via the O-acetyltransferase enzyme was sufficient to induce PTI. In the case of β -1,3/1,4-MLG, Rebaque et al. [19] demonstrated that the trisaccharide MLG43 (β -D-cellobiosyl-(1,3)- β -D-glucose) was the smallest unit form of these molecules to activate ROS burst in Arabidopsis leaf discs. In Arabidopsis, application of tetrasaccharide MLG elicited MAPK3/6 phosphorylation, which was almost negligible in response to trisaccharide MLG elicitation [112]. In contrast, both the tri- and tetrasaccharide MLG have triggered the phosphorylation of MAPK in barley [112].

6.2. Oligogalacturonides

OGAs, which are pectin derivatives generated during pathogenesis, act as DAMP agents to activate plant defense responses. They can be produced by the chemical or enzymatic hydrolysis of pectin. Application of purified OGAs has effectively induced stress tolerance mechanisms in different plant species [99,165,267,268] (Table 2). It was reported that only long OGAs with DP 10–15 are effective at inducing plant defense-related responses [269–271]. Importantly, short OGA oligomers with DP < 10 also showed efficient plant defense elicitation activity [184,186,262]. In another report, very short OGAs (DP1-3) were unable to induce the expression of genes encoding aminocyclopropane 1-carboxylic acid oxidase in tomato plants [272]. On the other hand, Davidsson et al. [99] found that trigalacturonic acid with DP 3 significantly triggered the expression of defense-related genes in a manner similar to long OGAs in Arabidopsis. Recently, short oligomers of OGAs with DP 6–9 showed better gray mold decay control in tomato fruits when compared with longer OGAs [100]. To the contrary, OGAs with DP 10–15 more efficiently triggered callose deposition than those with DP 3 and DP 25–50 in Arabidopsis against aphids [185]. Interestingly, a specific OGA degrading enzyme (oligogalacturonide oxidase 1) identified in Arabidopsis [273] showed the highest oxidizing activity on OGAs with DP 5 than those with DP 2–4 [274]. These findings showed that the elicitation potential of OGAs depends closely on their DP.

It was observed that enzymatic partial demethylation of OGA was required to induce resistance in strawberry against *Botrytis cinerea* [275]. Randoux et al. [98] found that both nonacetylated and 30 % acetylated OGAs elicited defensive enzymes in wheat. However, only the acetylated OGA led to an increased reduction of the formed fungal haustoria [98]. Likewise, pea plants treated with 30 % acetylated OGAs have shown an improved defense response than the nonacetylated OGA-treated groups against *A. euteiches* [268]. Thus, the methylation and acetylation degrees does clearly influence the plant disease resistance induction capability of OGAs.

6.3. β -1,3-glucans

β -1,3-glucans, originated from fungal pathogens and from brown algal cell walls, have been implicated in triggering plant immunity [1,38,276]. Plants do not respond to structurally varied β -1,3-glucans in a similar manner. It was reported that laminaripentose was the least to elicit PAL activity in tobacco cells; laminarin tetramer and trimer, however, showed weak and no elicitation activity, respectively [277]. Likewise, Mérida et al. [48] observed that laminaripentose was the least to induce defense-related responses in *A. thaliana*. The activity of short β -1,3-, 1,6-oligoglucan was more potent than that of longer laminarin in tobacco, which is a known elicitor of defense responses for this plant [276]. While barley and tobacco plants were responsive to long β -1,3-glucan (DP 7–16) rather than to shorter β -1,3-glucan (DP 6), the reverse was true for *A. thaliana* and *Capsella rubella* [38]. According to Klarzynski et al. [277], linear laminaripentose was a potent elicitor of PAL activity in tobacco cells, however, branched β -1,3-, 1,6-heptaglucan was inactive. Similarly, *C. rubella* responds with ROS burst to linear β -1,3-glucan but not to branched β -1,3-glucan [38]. To the contrary, both branched and non-branched β -1,3-glucans have induced immune-associated responses in *A. thaliana* [48] and tobacco [38]. For elicitation activity, the 1,6-linked and non-reducing terminal residues of β -1,3,1,6-oligoglucans were indispensable in tobacco [276] not the β -1,6-glycosidic side-branches, rather the polymer length was essential for laminarin treated tobacco plants [38, 278]. Chemical modification of laminarin with sulfate positively influenced its bioactivity [278,279]. Overall, the bioactivity of β -1,3-glucans is closely dependent on their sugar chain length, sulfate content, presence/absence of branching, and degree of branching. Further, Mérida et al. [48] detected a weak Ca^{2+} influx in *A. thaliana* Col-0 in response to laminarin treatment; however, Wanke et al. [38] observed that this plant did not respond to the same treatment. Thus, the growth condition, developmental stage, and treatment time could be other limiting factors for the bioactivity of β -1,3-glucan-based elicitors.

6.4. Ulvans

Applications of the green algae-derived ulvans and oligoulvans to various plant species have shown improved defense responses [280–284]. The bioactivity of ulvans, however, depends on their sugar composition, sulfate content, and molecular size. It was reported that sulfate residue is required for oligoulvan to induce defense-related genes expression [285–287]. In contrast, non-sulfated ulvan dimer showed elicitation activity in suspension-cultured cells of dicot plants in a manner similar to sulfated polymers [163]. With regard to DP, El Modafar et al. [286] reported that sulfated oligoglucuronans with DP 2–3 had more effective PAL induction capability than ulvan polymers in tomato seedlings. Likewise, sulfated oligoulvan with DP 2 showed better elicitation capability than the native ulvan in apple fruits to control decay [287]. Furthermore, it was suggested that the effective elicitation activity of ulvans might be related to their high rhamnose and/or uronic acid content [222,288]. Recently, de Borba et al. [182] corroborated that ulvan oligosaccharides with high rhamnose and/or uronic acid residues effectively elicited complex defense responses in wheat seedlings.

6.5. Carrageenans

Sulfated carrageenans extracted from the cell walls of some red algae have been shown to be potent plant defense elicitors [11,223, 289] and (Table 2). Compared to laminarin, only λ -carrageenan elicited an array of defense responses in tobacco leaves, possibly due to its high sulfate content [290]. Similarly, Le Mire et al. [223] demonstrated that λ -carrageenan showed greater elicitor capability in wheat to resist *Z. tritici* compared with other bioelicitors tested. Among the sulfated κ , λ , and ι -carrageenan types, λ -carrageenan with the highest sulfate content induces increased disease resistance in Arabidopsis, tomato, and tobacco plants [291–293]. By contrast, Arabidopsis plants treated with ι - and κ -carrageenans showed reduced leaf damage caused by *Trichoplusia ni* as compared with those λ -carrageenan-treated groups [294]. Recently, Pettongkhao et al. [181] reported that the sulfated λ -carrageenan exhibited the highest elicitation and resistance to *Phytophthora palmivora* infection in rubber tree leaves, whereas the desulphated polysaccharides did not. These findings indicated that the bioactivities of carrageenans relied on the sulfate content, treated plant type, and targeted phytopathogen.

6.6. Chitin and chitosan

To understand the structure-activity relationships of chitin/chitosan, a number of experiments focused on the structural factors, including DP, degree of acetylation (DA), and pattern of acetylation (PA) effect, on the bioactivity of chitin/chitosan were carried out. Brulé et al. [52] reported that CO with DP 6 was effective in activating the MAPK cascade and defensive responses. Whereas, Gubaeva et al. [166] observed that chitosan (DA 35 %) elicitation activity required a minimum of DP 9, and a maximum response was reached with DP 14. Besides, chitosan with DP 4 to 14–17 at DA 10 % were unable to induce defense responses [166]. The elicitor activity of chitosan increased with an increasing degree of acetylation of chitosan polymers, from 0 % to 35 % [166]. However, fully deacetylated chitosan (DP 3–8) was unable to induce defense responses in *A. thaliana* seedlings [166]. Similarly, Li et al. [295] used three hexamers, i.e., fully deacetylated chitosan (0 % DA), partially deacetylated chitosan (32.2 % DA), and fully acetylated chitin (100 % DA), with similar DP to investigate the role of DA on wheat seedling growth promotion activity. The results indicated that higher vegetative and photosynthetic parameters were recorded in the fully deacetylated chitosan-treated seedlings, followed by the partially de-acetylated and fully acetylated hexamers-treated groups, respectively. Likewise, the receptor binding ability of the de-acetylated chitin oligomer was better than that of the acetylated chitin oligomer with the same DP 8 [55]. Induced defense by mono-acetylated chitosan tetramers in rice cells was attained when the acetyl group was at or next to the non-reducing end unit, but not if it was at or next to the reducing end unit [296]. These findings indicated that the bioactivity of chitin/chitosan closely depends on its DP, DA, and PA. It was suggested

that these factors influence the overall charge of the molecule, which in turn determines its structure and then its function [296]. Though Kappel et al. [224] demonstrated that chitosan at a high molecular weight showed better fungicidal activity in an *in vitro* test, a low molecular weight of chitosan is generally accepted for plant immunity elicitation [196,296].

7. Carbohydrate-formulated commercial products application for plant protection

Many carbohydrates have been reported as potent plant immunity inducers (Table 2); however, only a few carbohydrate elicitors have been marketed so far. Indeed, the available carbohydrate-formulated products have been used on a limited scale, probably due to unsatisfactory efficiency, metabolic cost, and high competition with conventional synthetic fungicides and resistance inducers [228]. On the other hand, the European Commission has imposed restrictions on the application of synthetic chemicals for plant protection (Directive 2009/128/EC). This initiated looking for alternatives like the carbohydrate-formulated products, i.e., Vacciplant®, FytoSave®, and FytoSol®, which have been tested for their efficacy to control economically important phytopathogens.

Vacciplant® is the first commercially available carbohydrate-based formulation product with 45 g/L of brown algae-derived laminarin that has been approved for bio-protection in plants [223]. It is used to control olive leaf spot [297] and powdery mildew on strawberries, apples, and other crops [298]. Under field trial, weekly foliar sprays of Vacciplant® on leaves of grapevine provide reduced powdery mildew disease incidence (54.3 %) and severity (94.5 %) during a season with an increased presence of the disease [183]. Similarly, treatment using Vacciplant® was effective in controlling both powdery mildew and downy mildew on grapevines in a field trial [299]. In wheat, a single foliar spraying of Vacciplant® two days prior to *Z. tritici* inoculation significantly reduced both disease severity and pycnidium density in leaves at 21 days following infection under greenhouse conditions [228]. Vacciplant® conferred protection on wheat against *Z. tritici* through direct fungicidal activity and elicitation, but not priming, plant defense-related genes expression [228]. In addition, Vacciplant® did not significantly influence the production of plant metabolites, vigor, or yield [228,299,300], indicating that it specifically induced resistance without causing major metabolic cost to the plant. Vacciplant® has a limited confirmed effect on the berry transcriptome profile at the end of the season, revealing the long-term impact of its application [301].

The complex of chitoooligosaccharides and pectin-derived OGA (COS-OGA) at 12.5 g/L is an active component of the commercialized products FytoSave® and FytoSol®. It is believed that COS-OGA could activate a combined signal by alerting the presence of both cell-wall breakdown and pathogen infection, evoking a significantly stronger response than each factor acting independently [302]. FytoSave® induces the resistance of grapevines, cucumber, and tomato against powdery mildew [210,303]. Similarly, FytoSave® showed significantly improved protection of potato (~50 %) against late blight compared to untreated control under greenhouse conditions [304]. However, in controlling the late blight of potato, FytoSave® provided only 29 % of protection, which was far from 100 % protection obtained from FytoSol® spraying [211]. Likewise, sprayed FytoSol® was effective in controlling root-knot nematode infection and early blight in rice and tomato, respectively [177,176]. The effective protection provided by FytoSol® was associated with its direct fungicidal activity against *Phytophthora infestans* [211], which is not observed in FytoSave® [304]. COS-OGA-treated plants showed increased disease severity over time, suggesting that frequent spraying almost the whole season was required for effective protection [211,177]. Importantly, COS-OGA application reversed the fresh weight of tomato plants impaired due to a disease, also didn't affect the plant's growth parameters, including biomass accumulation on uninfected healthy plants [177]. Similarly, three-times foliar elicitation of tomato by the COS-OGA modulated the electron transport chain in thylakoids and the apoplast's redox homeostasis, inducing a long-term acclimation of plants without impairing biomass accumulation [305]. Therefore, application of these plant resistance inducers could provide compensated metabolic costs, energy allocation, and eliciting defense-related metabolites.

In foliar applications tested under both controlled and field conditions, carbohydrate elicitor-induced resistance was found to be dose-dependent [162,165,211,303] and generally showed inconsistency [183,303]. In addition, these carbohydrate-based plant resistance inducers may not always be as efficient as conventional synthetic chemicals in protecting plants. For example, in reducing powdery mildew on strawberries, foliar application of Vacciplant® allowed an infestation rate of 10.5 %, which was considerably better than the control, but worse than the chemical treatment [306]. In this context, carbohydrate elicitors should not be viewed as a one-size-fits-all solution, and integrated application strategies of carbohydrate elicitors in conjunction with or in rotation with other plant protection agents are preferred to improve their plant protection efficacy. For example, FytoSol® combined with a chemical pesticide showed enhanced plant disease resistance and reduced chemical pesticide usage [211]. Similarly, in grapevines, Vacciplant® mixed with a half dosage rate of a copper product demonstrated effective protection against downy mildew in outdoor and indoor trials [307,308]. The elicitation activity of the copper-combined laminarin was detected within one day of the treatment and continued until nine days [308]. Moreover, Vacciplant® and chitosan demonstrated better plant protection efficacy when combined with biological control agents (such as *Bacillus amyloliquefaciens* and *Trichoderma atroviride*) and brown algae (*Ascophyllum nodosum*) extract against leaf spot on olives and sugar beet and against powdery mildew on pea, respectively [214,224,297].

The aerial parts of plants are home to diverse microbial communities that are able to impact the development, growth, and health of plants through interacting with each other or with their host [309]. As discussed above, carbohydrate-based elicitors are becoming an integral part of sustainable plant protection strategies. However, the impact of sprayed carbohydrate elicitors on leaf-associated microbes along with their elicitation activities received little attention. Recently, Nerva et al. [310] observed that Vacciplant® leaf application against powdery mildew on grapevine did not influence both leaf-associated ecto- and endophytic microbial communities. Likewise, the leaf-associated microbial communities of grapevine were slightly influenced by the sprayed chitosan and polysaccharides extracted from *Rugulopteryx okamurae* and *Ulva ohnoi*, brown and green seaweeds, respectively [22,311]. Therefore, in order to be effective and helpful for application, carbohydrate elicitors would be investigated not only for their potential as resistance inducers, but also for their effects on phyllosphere microbial diversity.

8. Conclusions and prospects

In any country, making agricultural productivity sustainable is highly needed to address food security challenges. Treatments that improve plant health, growth, and yield while remaining cost and environmentally viable can greatly aid in the development of sustainable agriculture. In this scenario, the application of carbohydrate elicitors is pivotal to making agriculture sustainable and healthiest. Carbohydrate elicitor treatments provide efficient plant protection against various biotic and abiotic stresses. To initiate defense responses, plants are capable of detecting carbohydrate elicitors using their PRRs, mainly the LysM-containing PRRs. Carbohydrate elicitor perception system, enabling plants to recognize separate but structurally related molecules is complex and diversified among and within plant species. Therefore, further broad and in-depth investigation to further elucidate the role of carbohydrate-elicitor specific receptors in plant defense systems, mainly in economically important plant species, is needed. Following detection, the carbohydrate elicitors follow different PRR-downstream signaling pathways. The carbohydrate-elicitor-induced intense defense responses in different plant species depend on plant genotype, elicitor type, pathogen infection strategy, and environment. Thus, identifying the range of activated signals and having a detailed understanding of how a plant responds to these cascaded cues is crucial to formulating carbohydrate-based elicitors. Deployment of the recent advent of the tools of *omics* and their integrative (multi-*omics*) approach would be worthy to explore the carbohydrate elicitor-induced holistic and unknown metabolic discourse in a plant. Besides understanding the bioactivity and mechanisms of carbohydrate elicitors, developing an efficient delivery system is also valuable to enhance their efficacy mainly at field level. Luckily, the field of nanotechnology has opened new methods for designing nano-carbohydrate elicitors and field-level delivery system. However, information on the field application of nano-carbohydrate elicitors as plant defense elicitors in a wide range of plant species is minimal, and thus more work are expected. In addition to plant immunity signaling, carbohydrates have been shown to promote symbiosis signaling during interaction with beneficial microbes, though the interplay between symbiosis and immunity induction still requires further investigation. The striking bioactivities of carbohydrate elicitors depend on their structural features, so deciphering the structure-activity interactions is crucial to formulating carbohydrate-based plant immunity elicitors. Micronutrients such as iron, manganese, and zinc are involved in plant immune responses. Understanding the impact of soil micronutrients on carbohydrate elicitor-induced resistance efficacy in plants could further provide new insights. It would be interesting to explore the possibility of developing cross-tolerance towards biotic and abiotic stress conditions in primed plants. Moreover, the inheritance potential of the carbohydrate-elicitor-induced plant resistance phenotype to subsequent progeny as well as the underlying molecular mechanisms have yet to be fully investigated.

Mostly, the carbohydrate-elicitor-induced resistance is tested in greenhouses or under limited agricultural conditions, with a focus on narrow agricultural systems. So, exploring its effectiveness and feasibility in different agro-ecological conditions and agricultural systems can expand the scope of carbohydrate elicitors in agricultural productivity. In addition, understanding their potential use as biological plant protection agents, when formulated with other natural compounds or biological control agents, will be the key in order to incorporate them as effective and useful in agricultural practices.

Even though numerous carbohydrates have been reported to induce plant defense activities, only a few are formulated and licensed for plant protection and are generally used on a limited scale. They exhibit inconsistent efficiency on their own, mainly at field. Elucidating the elicitor x plant genotype x environment (biotic and abiotic factors) interaction could help in integrating the carbohydrate-formulated commercial products as component of sustainable plant protection strategies. Developing and implementing standards and techniques to certify effective carbohydrate-based elicitors as plant protection agents could also facilitate their production on a large scale and marketing. To identify most efficient carbohydrate elicitors, design screens and execute test mechanisms would be another important future challenge. In addition, farmers may incorporate carbohydrate elicitors into their plant stress management programs by giving information about the advantages, application mode, and best practices for carbohydrate elicitor treatments. Thus, it is necessary to provide training programs for farmers to adopt carbohydrate elicitors.

Funding statement

The authors did not receive any funding for this work.

Data availability statement

The data used to support the findings of this study are openly available in the listed references.

CRedit authorship contribution statement

Birhanu Kahsay Meresa: Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Kiros-Meles Ayimut:** Writing – review & editing, Methodology, Conceptualization. **Micheale Yifter Weldemichael:** Writing – review & editing. **Kalayou Hiluf Geberemedhin:** Writing – review & editing. **Hagos Hailu Kassegn:** Writing – review & editing, Methodology. **Bruh Asmelash Geberemikael:** Writing – review & editing. **Etsay Mesele Egiu:** Resources.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

The authors would like to appreciate and acknowledge the-Community Energy and Sustainable Energy Transition in Ethiopia, Malawi, and Mozambique (CESET) project funded by a grant from UK Research and Innovation and the Global Challenge Research Fund: ES/T006358/1 for financing the internet access to develop this review paper. Preparation of this paper would have been impossible in a time of lack of access to internet because of the complete blockage of all types of communication in the Tigray region. The authors would also like to acknowledge the reviewers for their constructive and collegial comments on this work.

References

- [1] C. Chaliha, M.D. Rugen, R.A. Field, E. Kalita, T. Mitchell, Glycans as modulators of plant defense against filamentous pathogens, *Front. Plant Sci.* 9 (928) (2018), <https://doi.org/10.3389/fpls.2018.00928>.
- [2] E. Quintana-Rodriguez, D. Duran-Flores, M. Heil, X. Camacho-Coronel, Damage-associated molecular patterns (DAMPs) as future plant vaccines that protect crops from pests, *Sci. Hortic.* 237 (2018) 207–220, <https://doi.org/10.1016/j.scienta.2018.03.026>.
- [3] N.A.A. Malik, I.S. Kumar, K. Nadarajah, Elicitor and receptor molecules: orchestrators of plant defense and immunity, *Int. J. Mol. Sci.* 21 (963) (2020), <https://doi.org/10.3390/ijms21030963>.
- [4] J.D.G. Jones, J.L. Dangl, The plant immune system, *Nature* 444 (16) (2006) 323–329, <https://doi.org/10.1038/nature05286>.
- [5] Y.C. Chen, E.C. Holmes, J. Rajniak, J.G. Kim, S. Tang, C.R. Fischer, et al., N-hydroxy-pipecolic acid is a mobile metabolite that induces systemic disease resistance in Arabidopsis, *Proc. Natl. Acad. Sci. U.S.A.* 115 (21) (2018) E4920–E4929, <https://doi.org/10.1073/pnas.1805291115>.
- [6] R. Sahu, M. Sharaff, M. Pradhan, A. Sethi, T. Bandyopadhyay, V.K. Mishra, Elucidation of defense-related signaling responses to spot blotch infection in bread wheat (*Triticum aestivum* L.), *Plant J.* 86 (2016) 35–49, <https://doi.org/10.1111/tj.13149>.
- [7] P.N. Dodds, J.P. Rathjen, Plant immunity: towards an integrated view of plant-pathogen interactions, *Nat. Rev. Genet.* 11 (8) (2010) 539–548, <https://doi.org/10.1038/nrg2812>.
- [8] T. Kawasaki, PRR cross-talk jump starts plant immunity, *Cell Host Microbe* 26 (6) (2019) 707–709, <https://doi.org/10.1016/j.chom.2019.11.007>.
- [9] Y. Wu, Y. Lin, H. Chuang, Laminarin modulates the chloroplast antioxidant system to enhance abiotic stress tolerance partially through the regulation of the defensin-like gene expression, *Plant Sci.* 247 (2016) 83–92, <https://doi.org/10.1016/j.plantsci.2016.03.008>.
- [10] N. Nejat, J. Rookes, N.L. Mantri, D.M. Cahill, Plant–pathogen interactions: toward development of next-generation disease-resistant plants, *Crit. Rev. Biotechnol.* 37 (2) (2016) 229–237, <https://doi.org/10.3109/07388551.2015.1134437>.
- [11] S. Trouvelot, M. Héloir, B. Poinsot, A. Gauthier, F. Paris, C. Guillier, et al., Carbohydrates in plant immunity and plant protection: roles and potential application as foliar sprays, *Front. Plant Sci.* 5 (2014) 592, <https://doi.org/10.3389/fpls.2014.00592>.
- [12] H.W. Choi, D.F. Klessig, DAMPs, MAMPs, and NAMPs in plant innate immunity, *BMC Plant Biol.* 16 (2016) 1–10, <https://doi.org/10.1186/s12870-016-0921-2>.
- [13] F. Zheng, L. Chen, P. Zhang, J. Zhou, X. Lu, W. Tian, Carbohydrate polymers exhibit great potential as effective elicitors in organic agriculture: a review, *Carbohydr. Polym.* 230 (2020) 115637, <https://doi.org/10.1016/j.carbpol.2019.115637>.
- [14] A. Hidayatmayum, P. Dwivedi, D. Katiyar, Application of chitosan on plant responses with special reference to abiotic stress, *Physiol. Mol. Biol. Plants* (2019), <https://doi.org/10.1007/s12298-018-0633-1>.
- [15] J. Claverie, S. Balacey, C. Lemaître-guillier, D. Brulé, A. Chiltz, L. Granet, et al., The cell wall-derived xyloglucan is a new DAMP triggering plant immunity in *Vitis vinifera* and *Arabidopsis thaliana*, *Front. Plant Sci.* 9 (2018) 1725, <https://doi.org/10.3389/fpls.2018.01725>.
- [16] H. Zang, S. Xie, B. Zhu, X. Yang, C. Gu, B. Hu, et al., Mannan oligosaccharides trigger multiple defence responses in rice and tobacco as a novel danger-associated molecular pattern, *Mol. Plant Pathol.* 20 (8) (2019) 1067–1079, <https://doi.org/10.1111/mpp.12811>.
- [17] H. Mérida, L. Bacete, C. Ruprecht, D. Rebaque, I. del Hierro, G. López, et al., Arabinoxylan-oligosaccharides act as damage associated molecular patterns in plants regulating disease resistance, *Front. Plant Sci.* 11 (2020) 1210, <https://doi.org/10.3389/fpls.2020.01210>.
- [18] C. Yang, R. Liu, J. Pang, B. Ren, H. Zhou, J. Liu, et al., Poaceae-specific cell wall-derived oligosaccharides activate plant immunity via OsCERK1 during *Magnaporthe oryzae* infection in rice, *Nat. Commun.* 12 (2021) 2178, <https://doi.org/10.1038/s41467-021-22456-x>.
- [19] D. Rebaque, I. del Hierro, G. López, L. Bacete, F. Vilaplana, P. Dallabernardina, et al., Cell wall-derived mixed-linked β -1,3/1,4-glucans trigger immune responses and disease resistance in plants, *Plant J.* 106 (2021) 601–615, <https://doi.org/10.1111/tj.15185>.
- [20] Y. Sun, H. Wu, S. Xu, S. Tang, J. Hao, X. Liu, et al., Roles of the EPS66A polysaccharide from *Streptomyces* sp. in inducing tobacco resistance to tobacco mosaic virus, *Int. J. Biol. Macromol.* 209 (2022) 885–894, <https://doi.org/10.1016/j.ijbiomac.2022.04.081>.
- [21] F. Rachidi, R. Benhima, Y. Kasmí, L. Sbabou, H. El Arroussi, Evaluation of microalgae polysaccharides as biostimulants of tomato plant defense using metabolomics and biochemical approaches, *Sci. Rep.* 11 (30) (2021), <https://doi.org/10.1038/s41598-020-78820-2>.
- [22] I. Zarrainandia, E. Cretazzo, A. Mena-Petite, A.M. Díez-Navajas, U. Pérez-López, M. Lacuesta, et al., Holistic understanding of the response of grapevines to foliar application of seaweed extracts, *Front. Plant Sci.* 14 (2023) 1119854, <https://doi.org/10.3389/fpls.2023.1119854>.
- [23] R. Gupta, S.E. Lee, G.K. Agrawal, R. Rakwal, S. Park, Y. Wang, et al., Understanding the plant-pathogen interactions in the context of proteomics-generated apoplast proteins inventory, *Front. Plant Sci.* 6 (2015) 352, <https://doi.org/10.3389/fpls.2015.00352>.
- [24] T. Kawasaki, K. Yamada, S. Yoshimura, K. Yamaguchi, Chitin receptor-mediated activation of MAP kinases and ROS production in rice and Arabidopsis, *Plant Signal. Behav.* 2324 (2017), <https://doi.org/10.1080/15592324.2017.1361076>.
- [25] J. Wang, J. Chai, Structural insights into the plant immune receptors PRRs, *Plant Physiol.* 182 (2020) 1566–1581, <https://doi.org/10.1104/pp.19.01252>.
- [26] L. Li, Y. Yu, Z. Zhou, J. Zhou, Plant pattern-recognition receptors controlling innate immunity, *Sci. China Life Sci.* 59 (9) (2016) 878–888, <https://doi.org/10.1007/s11427-016-0115-2>.
- [27] W. Wang, C. Xue, X. Mao, Chitosan: structural modification, biological activity and application, *Int. J. Biol. Macromol.* 164 (2020) 4532–4546, <https://doi.org/10.1016/j.ijbiomac.2020.09.042>.
- [28] Y. Desaki, M. Kohari, N. Shibuya, H. Kaku, MAMP-triggered plant immunity mediated by the LysM-receptor kinase CERK1, *J. Gen. Plant Pathol.* 85 (2019) 1–11, <https://doi.org/10.1007/s10327-018-0828-x>.
- [29] Y. Desaki, S. Takahashi, K. Sato, K. Maeda, S. Matsui, I. Yoshimi, et al., PUB4, a CERK1-interacting ubiquitin ligase, positively regulates MAMP-triggered immunity in Arabidopsis, *Plant Cell Physiol.* 60 (11) (2019) 2573–2583, <https://doi.org/10.1093/pcp/pcz151>.
- [30] B.P.M. Ngou, P. Ding, J.D.G. Jones, Thirty years of resistance: zig-zag through the plant immune system, *Plant Cell* 34 (2022) 1447–1478, <https://doi.org/10.1093/pcell/koac041>.
- [31] T. Shimizu, T. Nakano, D. Takamizawa, Y. Desaki, N. Ishii-Minami, Y. Nishizawa, et al., Two LysM receptor molecules, CEBIP and OsCERK1, cooperatively regulate chitin elicitor signaling in rice, *Plant J.* 64 (2) (2010) 204–214, <https://doi.org/10.1111/j.1365-3113.2010.04324.x>.
- [32] T. Shinya, N. Motoyama, A. Ikeda, M. Wada, K. Kamiya, M. Hayafune, et al., Functional characterization of CEBIP and CERK1 homologs in Arabidopsis and rice reveals the presence of different chitin receptor systems in plants, *Plant Cell Physiol.* 53 (10) (2012) 1696–1706, <https://doi.org/10.1093/pcp/pcs113>.
- [33] Y. Narusaka, T. Shinya, M. Narusaka, N. Motoyama, H. Shimada, K. Murakami, et al., Presence of LYM2 dependent but CERK1 independent disease resistance in Arabidopsis, *Plant Signal. Behav.* 8 (9) (2013), <https://doi.org/10.4161/psb.25345>.
- [34] Y. Kouzai, K. Nakajima, M. Hayafune, K. Ozawa, H. Kaku, N. Shibuya, et al., CEBIP is the major chitin oligomer-binding protein in rice and plays a main role in the perception of chitin oligomers, *Plant Mol. Biol.* 84 (2014) 519–528, <https://doi.org/10.1007/s11103-013-0149-6>.

- [35] B. Liu, J. Li, Y. Ao, J. Qu, Z. Li, J. Su, et al., Lysin motif-containing proteins LYP4 and LYP6 play dual roles in peptidoglycan and chitin perception in rice innate immunity, *Plant Cell* 24 (2012) 3406–3419, <https://doi.org/10.1105/tpc.112.102475>.
- [36] D. Tang, G. Wang, J.-M. Zhou, Receptor kinases in plant-pathogen interactions: more than pattern recognition, *Plant Cell* 29 (2017) 618–637, <https://doi.org/10.1105/tpc.16.00891>.
- [37] Y. Desaki, Y. Kouzai, Y. Ninomiya, R. Iwase, H. Kaku, Y. Nishizawa, OsCERK1 plays a crucial role in the lipopolysaccharide-induced immune response of rice, *New Phytol.* 217 (2018) 1042–1049, <https://doi.org/10.1111/nph.14941>.
- [38] A. Wanke, H. Rovenich, F. Schwanke, S. Veltz, S. Becker, J. Hehemann, et al., Plant species-specific recognition of long and short β -1, 3-linked glucans is mediated by different receptor systems, *Plant J.* 102 (2020) 1142–1156, <https://doi.org/10.1111/tpj.14688>.
- [39] J. Wan, K. Tanaka, X. Zhang, G.H. Son, L. Brechenmacher, T. Hong, et al., LYK4, a lysin motif receptor-like kinase, is important for chitin signaling and plant innate immunity in *Arabidopsis*, *Plant Physiol.* 160 (2012) 396–406, <https://doi.org/10.1104/pp.112.201699>.
- [40] D.X. Xue, C.L. Li, Z.P. Xie, C. Staehelin, LYK4 is a component of a tripartite chitin receptor complex in *Arabidopsis thaliana*, *J. Exp. Bot.* 70 (2019) 5507–5516, <https://doi.org/10.1093/jxb/erz313>.
- [41] C. Paparella, D.V. Savatin, L. Marti, G. De Lorenzo, S. Ferrari, The *Arabidopsis* lysin motif-containing receptor-like kinase 3 regulates the cross talk between immunity and abscisic acid responses, *Plant Physiol.* 165 (2014) 262–276, <https://doi.org/10.1104/pp.113.233759>.
- [42] Y. Cao, Y. Liang, K. Tanaka, C.T. Nguyen, R.P. Jedrzejczak, A. Joachimiak, et al., The kinase LYK5 is a major chitin receptor in *Arabidopsis* and forms a chitin-induced complex with related kinase CERK1, *Elife* 2 (2014) 1–19, <https://doi.org/10.7554/eLife.03766>.
- [43] K. Yamada, K. Yamaguchi, T. Shirakawa, H. Nakagami, A. Mine, K. Ishikawa, et al., The *Arabidopsis* CERK1-associated kinase PBL 27 connects chitin perception to MAPK activation, *EMBO J.* 35 (22) (2016) 2468–2483, <https://doi.org/10.15252/embj.201694248>.
- [44] J. Erwig, H. Ghareeb, M. Kopschke, R. Hacke, A. Matei, E. Petutschnig, et al., Chitin-induced and chitin elicitor receptor kinase 1 (CERK1) phosphorylation-dependent endocytosis of *Arabidopsis thaliana* Lysin motif-containing receptor-like kinase5 (LYK5), *New Phytol.* 215 (2017) 382–396, <https://doi.org/10.1111/nph.14592>.
- [45] C.L. Li, D.X. Xue, Y.H. Wang, Z.P. Xie, C. Staehelin, A method for functional testing constitutive and ligand-induced interactions of lysin motif receptor proteins, *Plant Methods* 16 (3) (2020), <https://doi.org/10.1186/s13007-020-0551-4>.
- [46] M. Giovannoni, D. Lironi, L. Marti, C. Paparella, V. Vecchi, A.A. Gust, et al., The *Arabidopsis thaliana* LysM-containing Receptor-Like Kinase 2 is required for elicitor-induced resistance to pathogens, *Plant Cell Environ.* 44 (2021) 3775–3792, <https://doi.org/10.1111/pce.14192>.
- [47] R. Willmann, H.M. Lajunen, G. Erbs, M. Newman, D. Kolb, K. Tsuda, *Arabidopsis* lysin-motif proteins LYM1 LYM3 CERK1 mediate bacterial peptidoglycan sensing and immunity to bacterial infection, *Pro. Nat. Acad. Sci. USA* 108 (49) (2011) 19824–19829, <https://doi.org/10.1073/pnas.1112862108>.
- [48] H. Mérida, S. Sopena-Torres, L. Bacete, M. Garrido-Aranda, J. Jordá, G. López, et al., Non-branched β -1,3-glucan oligosaccharides trigger immune responses in *Arabidopsis*, *Plant J.* 93 (2018) 34–49, <https://doi.org/10.1111/tpj.13755>.
- [49] C. Espinoza, Y. Liang, G. Stacey, Chitin receptor CERK1 links salt stress and chitin-triggered innate immunity in *Arabidopsis*, *Plant J.* 89 (2017) 984–995, <https://doi.org/10.1111/tpj.13437>.
- [50] L. Chen, W. Xia, J. Song, M. Wu, Z. Xu, X. Hu, et al., The chitin-induced chimeric LYK4-ER gene improves the heat tolerance of *Arabidopsis* at the seedling stage, *J. Plant Biol.* 63 (2020) 279–288, <https://doi.org/10.1007/s12374-020-09249-3>.
- [51] E. Rolli, A. de Zélicourt, H. Alzubaidy, M. Karampelias, S. Parween, N. Rayapuram, et al., The Lys-motif receptor LYK4 mediates *Enterobacter* sp SA187 triggered salt in *Arabidopsis thaliana*, *Environ. Microbiol.* 24 (1) (2022) 223–239, <https://doi.org/10.1111/1462-2920.15839>.
- [52] D. Brulé, C. Villano, L.J. Davies, L. Trdá, J. Claverie, M.C. Héloir, et al., The grapevine *Vitis vinifera* LysM receptor kinases VvLYK1-1 and VvLYK1-2 mediate chitoooligosaccharide-triggered immunity, *Plant Biotechnol. J.* 17 (2019) 812–825, <https://doi.org/10.1111/pbi.13017>.
- [53] T. Roudaire, T. Marzari, D. Landry, B. Löffelhardt, A.A. Gust, A. Jermakow, The grapevine LysM receptor-like kinase VvLYK5-1 recognizes chitin oligomers through its association with VvLYK1-1, *Front. Plant Sci.* 14 (295) (2023), <https://doi.org/10.3389/fpls.2023.1130782>.
- [54] I.V. Leppyanen, V.Y. Shakhnazarova, O.Y. Shtark, N.A. Vishnevskaya, I.A. Tikhonovich, E.A. Dolgikh, Receptor-like kinase LYK9 in *Pisum sativum* L. is the CERK1-like receptor that controls both plant immunity and AM symbiosis development, *Int. J. Mol. Sci.* 19 (8) (2018), <https://doi.org/10.3390/ijms19010008>.
- [55] I.V. Leppyanen, O.A. Pavlova, M.A. Vashurina, A.D. Bovin, A.V. Dolgikh, O.Y. Shtark, et al., LysM Receptor-Like Kinase LYK9 of *Pisum Sativum* L. may regulate plant responses to chitoooligosaccharides differing in structure, *Int. J. Mol. Sci.* 22 (711) (2021), <https://doi.org/10.3390/ijms22020711>.
- [56] P.Y. Kozulina, O.A. Pavlova, E.S.K. Rudaya, A.D. Bovin, S.A. Shirobokova, A.V. Dolgikh, et al., Transcriptomic analysis of pea plant responses to chitoooligosaccharides' treatment revealed stimulation of mitogen-activated protein kinase cascade, *Front. Plant Sci.* 14 (1092013) (2023), <https://doi.org/10.3389/fpls.2023.1092013>.
- [57] Z. Gu, T. Liu, B. Ding, F. Li, Q. Wang, S. Qian, et al., Two lysin-motif receptor kinases, Gh-LYK1 and Gh-LYK2, contribute to resistance against *Verticillium* wilt in upland cotton, *Front. Plant Sci.* 8 (2017) 2133, <https://doi.org/10.3389/fpls.2017.02133>.
- [58] P. Wang, L. Zhou, P. Jamieson, L. Zhang, Z. Zhao, K. Babilonia, et al., The cotton wall-associated kinase GhWAK7A mediates responses to fungal wilt pathogens by complexing with the chitin sensory receptors, *Plant Cell* 32 (12) (2020) 3978–4001, <https://doi.org/10.1105/tpc.19.00950>.
- [59] D. Liao, X. Sun, N. Wang, F. Song, Y. Liang, Tomato LysM receptor-like kinase SILYK12 is involved in *Arbuscular mycorrhizal* symbiosis, *Front. Plant Sci.* 9 (1004) (2018), <https://doi.org/10.3389/fpls.2018.01004>.
- [60] Y. Ai, Q. Li, C. Li, R. Wang, X. Sun, S. Chen, et al., Tomato LysM receptor kinase 4 mediates chitin-elicited fungal resistance in both leaves and fruit, *Hortic. Res.* 2023 (2023), <https://doi.org/10.1093/hr/uhad082>.
- [61] Z. Lv, Y. Ma, B. Huang, Z. Xiang, N. He, LysM1 in MmLYK2 is a motif required for the interaction of MmLYP1 and MmLYK2 in the chitin signaling, *Plant Cell Rep.* 37 (2018) 1101–1112, <https://doi.org/10.1007/s00299-018-2295-4>.
- [62] Z. Bozsoki, J. Cheng, F. Feng, K. Gysel, M. Vinther, K.R. Andersen, et al., Receptor-mediated chitin perception in legume roots is functionally separable from Nod factor perception, *Proc. Natl. Acad. Sci. U.S.A.* (2017) E8118–E8127, <https://doi.org/10.1073/pnas.1706795114>.
- [63] L. Zhang, L. Yuan, C. Staehelin, Y. Li, J. Ruan, Z. Liang, et al., The lysin motif-containing receptor-like kinase 1 protein of banana is required for perception of pathogenic and symbiotic signals, *New Phytol.* 223 (2019) 1530–1546, <https://doi.org/10.1111/nph.15888>.
- [64] M. de L. Santos, M.L.V. de Resende, B.A. dos Santos Ciscon, N.C. Freitas, M.H. de B. Pereira, T. Reichel, et al., LysM receptors in *Coffea arabica*: identification, characterization, and gene expression in response to *Hemileia vastatrix*, *PLoS One* 17 (2) (2022), <https://doi.org/10.1371/journal.pone.0258838>.
- [65] Z. Zhou, Y. Tian, P. Cong, Y. Zhu, Functional characterization of an apple (*Malus x domestica*) LysM domain receptor encoding gene for its role in defense response, *Plant Sci.* 269 (2018) 56–65, <https://doi.org/10.1016/j.plantsci.2018.01.006>.
- [66] Q. Chen, C. Dong, X. Sun, Y. Zhang, H. Dai, S. Bai, Overexpression of an apple LysM-containing protein gene, MdCERK1-2, confers improved resistance to the pathogenic fungus, *Alternaria alternata*, in *Nicotiana benthamiana*, *BMC Plant Biol.* 20 (146) (2020), <https://doi.org/10.1186/s12870-020-02361-z>.
- [67] H. Kaku, Y. Nishizawa, N. Ishii-Minami, C. Akimoto-Tomiya, N. Dohmae, K. Takio, et al., Plant cells recognize chitin fragments for defense signaling through a plasma membrane receptor, *Proc. Natl. Acad. Sci. U.S.A.* 103 (29) (2006) 11086–11091, <https://doi.org/10.1073/pnas.0508882103>.
- [68] J. Xu, G. Wang, J. Wang, Y. Li, L. Tian, X. Wang, W. Guo, et al., The lysin motif-containing proteins, Lyp1, Lyp7 and LysMe3, play important roles in chitin perception and defense against *Verticillium dahliae* in cotton, *BMC Plant Biol.* 17 (148) (2017), <https://doi.org/10.1186/s12870-017-1096-1>.
- [69] S. Tanaka, A. Ichikawa, K. Yamada, G. Tsuji, T. Nishiuchi, M. Mori, et al., HvCEBiP, a gene homologous to rice chitin receptor CEBiP, contributes to basal resistance of barley to *Magnaporthe oryzae*, *BMC Plant Biol.* 10 (288) (2010), <https://doi.org/10.1186/1471-2229-10-288>.
- [70] A. Fan, L. Wei, X. Zhang, J. Liu, L. Sun, J. Xiao, et al., Heterologous expression of the *Haynaldia villosa* pattern-recognition receptor CERK1-V in wheat increases resistance to three fungal diseases, *Crop J.* 10 (6) (2022) 1733–1745, <https://doi.org/10.1016/j.cj.2022.02.005>.
- [71] Y. Tseng, S.S. Scholz, J. Fliegmann, T. Krüger, A. Gandhi, A.C.U. Furch, et al., CORK1, a LRR-malectin receptor kinase, is required for cellooligomer-induced responses in *Arabidopsis thaliana*, *Cells* 11 (2960) (2022), <https://doi.org/10.3390/cells11192960>.

- [72] M. Martín-Dacal, P. Fernández-Calvo, P. Jiménez-Sandoval, G. López, M. Garrido-Arandía, D. Rebaque, Arabidopsis immune responses triggered by cellulose- and mixed-linked glucan-derived oligosaccharides require a group of leucine-rich repeat lectin receptor kinases, *Plant J.* 113 (2023) 833–850, <https://doi.org/10.1111/tpj.16088>.
- [73] I.S. Hwang, B.K. Hwang, The pepper mannose-binding lectin gene CaMBL1 is required to regulate cell death and defense responses to microbial pathogens, *Plant Physiol.* 155 (1) (2011) 447–463, <https://doi.org/10.1104/pp.110.164848>.
- [74] L. Ma, Z.M. Haile, S. Sabbadini, B. Mezzetti, F. Negrini, E. Baraldi, Functional characterization of Mannose-Binding Lectin 1, a G-type lectin gene family member, in response to fungal pathogens of strawberry, *J. Exp. Bot.* 74 (1) (2023) 149–161, <https://doi.org/10.1093/jxb/erac396>.
- [75] Y.-S. Dai, D. Liu, W. Guo, Z.-X. Liu, X. Zhang, L.-L. Shi, D.-M. Zhou, et al., Poaceae-specific β -1,3;1,4-D-glucans link jasmonate signalling to OsLecRK1-mediated defence response during rice-brown planthopper interactions, *Plant Biotechnol. J.* (2023) 1–15, <https://doi.org/10.1111/pbi.14038>.
- [76] A. Brutus, F. Sicilia, A. Macone, F. Cervone, G. de Lorenzo, A domain swap approach reveals a role of the plant wall-associated kinase 1 (WAK1) as a receptor of oligogalacturonides, *Proc. Natl. Acad. Sci. U.S.A.* 107 (20) (2010) 9452–9457, <https://doi.org/10.1073/pnas.1000675107>.
- [77] N. Jaiswal, C.-J. Liao, B. Mengesha, H. Han, S. Lee, A. Sharon, et al., Regulation of plant immunity and growth by tomato receptor-like cytoplasmic kinase TRK1, *New Phytol.* 2033 (2022) 458–478, <https://doi.org/10.1111/nph.17801>.
- [78] H. Yang, D. Wang, L. Guo, H. Pan, R. Yvon, S. Garman, et al., Malectin/Malectin-like domain-containing proteins: a repertoire of cell surface molecules with broad functional potential, *Cell Surf 7* (2021) 100056, <https://doi.org/10.1016/j.tcsv.2021.100056>.
- [79] I. del Hierro, M. Hugo, C. Broiyart, J. Santiago, A. Molina, Computational prediction method to decipher receptor-glycoligand interactions in plant immunity, *Plant J.* 105 (2021) 1710–1726, <https://doi.org/10.1111/tpj.15133>.
- [80] J. Wan, M. He, Q. Hou, L. Zou, Y. Yang, Y. Wei, et al., Cell wall associated immunity in plants, *Stress Biol* 1 (3) (2021), <https://doi.org/10.1007/s44154-021-00003-4>.
- [81] Y.H. Yeh, D. Panzeri, Y. Kadot, Y.C. Huang, P.Y. Huang, C.N. Tao, et al., The Arabidopsis malectin-like/LRR-RLK IOS1 is critical for BAK1-dependent and BAK1-independent pattern-triggered immunity, *Plant Cell* 28 (7) (2016) 1701–1721, <https://doi.org/10.1105/tpc.16.00313>.
- [82] W. Feng, D. Kita, A. Peaucelle, H.N. Cartwright, V. Doan, Q. Duan, et al., The FERONIA receptor kinase maintains cell-wall integrity during salt stress through Ca^{2+} signaling, *Curr. Biol.* 28 (5) (2018) 666–675, <https://doi.org/10.1016/j.cub.2018.01.023>.
- [83] W. Tang, W. Lin, X. Zhou, J. Guo, X. Dang, B. Li, et al., Mechano-transduction via the pectin-FERONIA complex activates ROP6 GTPase signaling in Arabidopsis pavement cell morphogenesis, *Curr. Biol.* 32 (3) (2022) 508–517, <https://doi.org/10.1016/j.cub.2021.11.031>.
- [84] C. Liu, H. Yu, A. Voxel, X. Rao, R.A. Dixon, FERONIA and wall-associated kinases coordinate defense induced by lignin modification in plant cell walls, *Sci. Adv.* 9 (2023), <https://doi.org/10.1126/sciadv.adf7714>.
- [85] M. Stegmann, J. Monaghan, E. Smakowska-Luzan, H. Rovenich, A. Lehner, N. Holton, et al., The receptor kinase FER is a RALF-regulated scaffold controlling plant immune signaling, *Science* 355 (2017) 287–289, <https://doi.org/10.1126/science.aal2541>.
- [86] Q. Duan, M.C.J. Liu, D. Kita, S.S. Jordan, F.L.J. Yeh, R. Yvon, et al., FERONIA controls pectin-and nitric oxide-mediated male-female interaction, *Nature* 579 (7800) (2020) 561–566, <https://doi.org/10.1038/s41586-020-2106-2>.
- [87] A. Gandhi, Y.-H. Tseng, R. Oelmüller, The damage-associated molecular pattern cellulose alters the phosphorylation pattern of proteins involved in cellulose synthesis and trans-Golgi trafficking in *Arabidopsis thaliana*, *Plant Signal. Behav.* 18 (1) (2023), <https://doi.org/10.1080/15592324.2023.2184352>.
- [88] Y. Sun, Z. Qiao, W. Muchero, J.G. Chen, Lectin receptor-like kinases: the sensor and mediator at the plant cell surface, *Front. Plant Sci.* 11 (2020) 596301, <https://doi.org/10.3389/fpls.2020.596301>.
- [89] E.J. Andersen, S. Ali, E. Byamukama, Y. Yen, M.P. Nepal, Disease resistance mechanisms in plants, *Genes* 9 (339) (2018), <https://doi.org/10.3390/genes9070339>.
- [90] S. Ranf, N. Gisch, M. Schäffer, T. Illig, L. Westphal, Y.A. Knirel, et al., A lectin S-domain receptor kinase mediates lipopolysaccharide sensing in *Arabidopsis thaliana*, *Nat. Immunol.* (2015), <https://doi.org/10.1038/ni.3124>.
- [91] A. Kutschera, C. Dawid, N. Gisch, C. Schmid, L. Raasch, T. Gerster, et al., Bacterial medium-chain 3-hydroxy fatty acid metabolites trigger immunity in Arabidopsis plants, *Plant Sci.* 364 (2019) 178–181, <https://doi.org/10.1126/science.aau1279>.
- [92] R.H. Hussan, I.A. Dubery, L.A. Piater, Identification of MAMP-responsive plasma membrane-associated proteins in *Arabidopsis thaliana* following challenge with different LPS chemotypes from *Xanthomonas campestris*, *Pathogens* 9 (10) (2020) 1–23, <https://doi.org/10.3390/pathogens9100787>.
- [93] N.M. Baloyi, I.A. Dubery, L.A. Piater, Proteomic analysis of Arabidopsis plasma membranes reveals lipopolysaccharide-responsive changes, *Biochem. Biophys. Res. Commun.* 486 (4) (2017) 1137–1142, <https://doi.org/10.1016/j.bbrc.2017.04.016>.
- [94] M.M. Tinte, P.A. Steenkamp, L.A. Piater, I.A. Dubery, Lipopolysaccharide perception in *Arabidopsis thaliana*: diverse LPS chemotypes from *Burkholderia cepacia*, *Pseudomonas syringae* and *Xanthomonas campestris* trigger differential defence-related perturbations in the metabolome, *Plant Physiol. Biochem.* 156 (2020) 267–277, <https://doi.org/10.1016/j.plaphy.2020.09.006>.
- [95] C. Castro, M. Massonnet, N. Her, B. DiSalvo, B. Jablonska, D.R. Jeske, et al., Priming grapevine with lipopolysaccharide confers systemic resistance to Pierce's disease and identifies a peroxidase linked to defense priming, *New Phytol.* (2023), <https://doi.org/10.1111/nph.18945>.
- [96] I. Kaloshian, L.L. Walling, Hemipteran and dipteran pests: effectors and plant host immune regulators, *J. Integr. Plant Biol.* 58 (4) (2016) 350–361, <https://doi.org/10.1111/jipb.12438>.
- [97] C. Stephens, K.E. Hammond-Kosack, K. Kanyuka, WAKs in plant immunity, waning diseases, *J. Exp. Bot.* 73 (1) (2022) 22–37, <https://doi.org/10.1093/jxb/erab422>.
- [98] B. Randoux, D. Renard-Merlier, G. Mulard, S. Rossard, F. Duyme, J. Sanssené, et al., Distinct defenses induced in wheat against powdery mildew by acetylated and nonacetylated oligogalacturonides, *Phytopathology* 100 (12) (2010) 1352–1363, <https://doi.org/10.1094/PHYTO-03-10-0086>.
- [99] P. Davidsson, M. Broberg, T. Kariola, N. Sipari, M. Pirhonen, E.T. Palva, Short oligogalacturonides induce pathogen resistance-associated gene expression in *Arabidopsis thaliana*, *BMC Plant Biol.* 17 (19) (2017), <https://doi.org/10.1186/s12870-016-0959-1>.
- [100] L. Lu, Y. Yang, H. Zhang, D. Sun, Z. Li, Q. Guo, et al., Oligogalacturonide-accelerated healing of mechanical wounding in tomato fruit requires calcium-dependent systemic acquired resistance, *Food Chem.* 337 (127992) (2021), <https://doi.org/10.1016/j.foodchem.2020.127992>.
- [101] B.D. Kohorn, B.E. Greed, G. Mouille, S. Verger, S.L. Kohorn, Effects of Arabidopsis wall associated kinase mutations on ESMEALDA1 and elicitor induced ROS, *PLoS One* 16 (5) (2021), <https://doi.org/10.1371/journal.pone.0251922>.
- [102] H. Qi, F. Guo, L. Lv, X. Zhu, L. Zhang, J. Yu, et al., The wheat wall-associated receptor-like kinase TaWAK-6D mediates broad resistance to two fungal pathogens *Fusarium pseudograminearum* and *Rhizoctonia cerealis*, *Front. Plant Sci.* 12 (2021) 758196, <https://doi.org/10.3389/fpls.2021.758196>.
- [103] H. Qi, X. Zhu, F. Guo, L. Lv, Z. Zhang, The wall-associated receptor-like kinase TaWAK7D is required for defense responses to *Rhizoctonia cerealis* in wheat, *Int. J. Mol. Sci.* 22 (5629) (2021), <https://doi.org/10.3390/ijms22115629>.
- [104] A. Delteil, E. Gobatto, B. Cayrol, J. Estevan, C. Michel-Romiti, A. Dievart, et al., Several wall-associated kinases participate positively and negatively in basal defense against rice blast fungus, *BMC Plant Biol.* 16 (17) (2016), <https://doi.org/10.1186/s12870-016-0711-x>.
- [105] F. Guo, T. Wu, G. Xu, H. Qi, X. Zhu, Z. Zhang, TaWAK2A-800, a wall-associated kinase, participates positively in resistance to fusarium head blight and sharp eyespot in wheat, *Int. J. Mol. Sci.* 22 (11493) (2021), <https://doi.org/10.3390/ijms22111493>.
- [106] A.I. Huerter, G. Sancho-Andres, J.C. Montesinos, J. Silva-Navas, S. Bassard, C. Pau-Roblot, et al., The WAK-like protein RFO1 acts as a sensor of the pectin methylation status in Arabidopsis cell walls to modulate root growth and defense, *Mol. Plant* 16 (2023) 865–881, <https://doi.org/10.1016/j.molp.2023.03.015>.
- [107] B.D. Kohorn, S. Johansen, A. Shishido, T. Todorova, R. Martinez, E. Defeo, et al., Pectin activation of MAP kinase and gene expression is WAK2 dependent, *Plant J.* 60 (2009) 974–982, <https://doi.org/10.1111/j.1365-313X.2009.04016.x>.
- [108] B.-Q. Gong, J. Guo, N. Zhang, X. Yao, H.-B. Wang, J.-F. Li, Cross-microbial protection via priming a conserved immune co-receptor through juxtamembrane phosphorylation in plants, *Cell Host Microbe* 26 (2019) 810–822, <https://doi.org/10.1016/j.chom.2019.10.010>.
- [109] M. Gravino, F. Locci, S. Tundo, F. Cervone, D.V. Savatin, G.D.E. Lorenzo, Immune responses induced by oligogalacturonides are differentially affected by AvrPto and loss of BAK1/BKK1 and PEPR1/PEPR2, *Mol. Plant Pathol.* 18 (4) (2017) 582–595, <https://doi.org/10.1111/mpp.12419>.

- [110] J.M. Johnson, J. Thürich, E.K. Petutschnig, L. Altschmied, D. Meichsner, I. Sherameti, et al., A Poly (A) ribonuclease controls the cellobiose-based interaction between *Piriformospora indica* and its host Arabidopsis, *Plant Physiol.* 176 (2018) 2496–2514, <https://doi.org/10.1104/pp.17.01423>.
- [111] C. de Azevedo Souza, S. Li, A.Z. Lin, F. Boutrot, G. Grossmann, C. Zipfel, et al., Cellulose-derived oligomers act as damage-associated molecular patterns and trigger defense-like responses, *Plant Physiol.* 173 (2017) 2383–2398, <https://doi.org/10.1104/pp.16.01680>.
- [112] S. Barghahn, G. Arnal, N. Jain, E. Petutschnig, H. Brumer, Mixed linkage β -1,3/1,4-glucan oligosaccharides induce defense responses in *Hordeum vulgare* and *Arabidopsis thaliana*, *Front. Plant Sci.* 12 (2021) 682439, <https://doi.org/10.3389/fpls.2021.682439>.
- [113] E.K. Petutschnig, A.M.E. Jones, L. Serazetdinova, U. Lipka, V. Lipka, The lysin motif receptor-like kinase (LysM-RLK) CERK1 is a major chitin-binding protein in *Arabidopsis thaliana* and subject to chitin-induced phosphorylation, *J. Biol. Chem.* 285 (37) (2010) 28902–28911, <https://doi.org/10.1074/jbc.M110.116657>.
- [114] M. Suzuki, M. Shibuya, H. Shimada, N. Motoyama, M. Nakashima, S. Takahashi, et al., Autophosphorylation of specific threonine and tyrosine residues in Arabidopsis CERK1 is essential for the activation of chitin-induced immune signaling, *Plant Cell Physiol.* 57 (11) (2016) 2312–2322, <https://doi.org/10.1093/pcp/pcw150>.
- [115] M. Suzuki, T. Watanabe, I. Yoshida, H. Kaku, N. Shibuya, Autophosphorylation site Y428 is essential for the in vivo activation of CERK1, *Plant Signal. Behav.* 13 (2) (2018), <https://doi.org/10.1080/15592324.2018.1435228>.
- [116] Q. Zhou, J. Liu, J. Wang, S. Chen, L. Chen, J. Wang, et al., The juxtamembrane domains of Arabidopsis CERK1, BAK1, and FLS2 play a conserved role in chitin-induced signaling, *J. Integr. Plant Biol.* 62 (5) (2020) 556–562, <https://doi.org/10.1111/jipb.12847>.
- [117] K. Yamaguchi, K. Yamada, K. Ishikawa, S. Yoshimura, N. Hayashi, K. Uchihashi, et al., A receptor-like cytoplasmic kinase targeted by a plant pathogen effector is directly phosphorylated by the chitin receptor and mediates rice immunity, *Cell Host Microbe* 13 (3) (2013) 347–357, <https://doi.org/10.1016/j.chom.2013.02.007>.
- [118] C. Wang, G. Wang, C. Zhang, P. Zhu, H. Dai, N. Yu, et al., OsCERK1-mediated chitin perception and immune signaling requires receptor-like cytoplasmic kinase 185 to activate an MAPK cascade in rice, *Mol. Plant* 10 (4) (2017) 619–633, <https://doi.org/10.1016/j.molp.2017.01.006>.
- [119] J. Wang, X. Liu, A. Zhang, Y. Ren, F. Wu, G. Wang, et al., A cyclic nucleotide-gated channel mediates cytoplasmic calcium elevation and disease resistance in rice, *Cell Res.* 29 (2019) 820–831, <https://doi.org/10.1038/s41422-019-0219-7>.
- [120] Z. Li, Y. Ao, D. Feng, J. Liu, J. Wang, H. Wang, et al., OsRLCK57, OsRLCK107 and OsRLCK118 positively regulate chitin- and PGN- induced immunity in rice, *Rice* 10 (6) (2017), <https://doi.org/10.1186/s12284-017-0145-6>.
- [121] J. Fan, P. Bai, Y. Ning, Y. Xia, L. Shan, G. Wang, et al., The monocot-specific receptor-like Kinase SDS2 controls cell death and immunity in rice, *Cell Host Microbe* 23 (4) (2018) 498–510, <https://doi.org/10.1016/j.chom.2018.03.003>.
- [122] X. Xiao, R. Wang, W. Guo, S. Khaskhali, R. Fan, R. Zhao, et al., The receptor-like cytoplasmic kinase OsRLCK118 regulates plant development and basal immunity in rice (*Oryza sativa* L.), *Trop. Plants* 1 (4) (2022), <https://doi.org/10.48130/TP-2022-0004>.
- [123] Y. Kanda, N. Yokotani, S. Maeda, Y. Nishizawa, M. Mori, The receptor-like cytoplasmic kinase BSR1 mediates chitin-induced defense signaling in rice cells, *Biosci. Biotechnol. Biochem.* 81 (8) (2017) 1497–1502, <https://doi.org/10.1080/09168451.2017.1325710>.
- [124] Y. Kanda, H. Nakagawa, Y. Nishizawa, T. Kamakura, Broad-spectrum disease resistance conferred by the overexpression of rice RLCK BSR1 results from an enhanced immune response to multiple MAMPs, *Int. J. Mol. Sci.* 20 (5523) (2019), <https://doi.org/10.3390/ijms20225523>.
- [125] S. Sugano, S. Maeda, N. Hayashi, H. Kajiwara, H. Inoue, C. Jiang, et al., Tyrosine phosphorylation of a receptor-like cytoplasmic kinase, BSR1, plays a crucial role in resistance to multiple pathogens in rice, *Plant J.* 96 (2018) 1137–1147, <https://doi.org/10.1111/tjp.14093>.
- [126] Y. Kanda, Y. Nishizawa, T. Kamakura, M. Mori, Overexpressed BSR1-mediated enhancement of disease resistance depends on the MAMP-recognition system, *Int. J. Mol. Sci.* 21 (5397) (2020), <https://doi.org/10.3390/ijms21155397>.
- [127] J. Wang, H. Shi, L. Zhou, C. Peng, D. Liu, X. Zhou, et al., OsBSK1-2, an orthologous of AtBSK1, is involved in rice immunity, *Front. Plant Sci.* 8 (2017) 908, <https://doi.org/10.3389/fpls.2017.00908>.
- [128] T. Shinya, K. Yamaguchi, Y. Desaki, K. Yamada, T. Narisawa, Y. Kobayashi, et al., Selective regulation of the chitin-induced defense response by the Arabidopsis receptor-like cytoplasmic kinase BBL27, *Plant J.* 79 (2014) 56–66, <https://doi.org/10.1111/tjp.12535>.
- [129] M. Suzuki, I. Yoshida, K. Suto, Y. Desaki, N. Shibuya, H. Kaku, AtCERK1 phosphorylation site S493 contributes to the transphosphorylation of downstream components for chitin-induced immune signaling, *Plant Cell Physiol.* 60 (8) (2019) 1804–1810, <https://doi.org/10.1093/pcp/pcz096>.
- [130] Y. Liu, T. Maierhofer, K. Rybak, J. Sklenar, A. Breakspear, M.G. Johnston, et al., Anion channel SLAH3 is a regulatory target of chitin receptor-associated kinase PBL27 in microbial stomatal closure, *Elife* 8 (2019), <https://doi.org/10.7554/eLife.44474>.
- [131] Y. Desaki, M. Morishima, Y. Sano, T. Uemura, A. Ito, K. Nemoto, et al., Cytoplasmic kinase network mediates defense response to *Spodoptera litura* in Arabidopsis, *Plants* 12 (1247) (2023), <https://doi.org/10.3390/plants12091747>.
- [132] S. Rao, Z. Zhou, P. Miao, G. Bi, M. Hu, Y. Wu, et al., Roles of receptor-like cytoplasmic kinase VII members in pattern-triggered immune signaling, *Plant Physiol.* 177 (2018) 1679–1690, <https://doi.org/10.1104/pp.18.00486>.
- [133] G. Bi, Z. Zhou, W. Wang, L. Li, S. Rao, Y. Wu, et al., Receptor-like cytoplasmic kinases directly link diverse pattern recognition receptors to the activation of mitogen-activated protein kinase cascades in Arabidopsis, *Plant Cell* 30 (2018) 1543–1561, <https://doi.org/10.1105/tpc.17.00981>.
- [134] Y. Li, J. Xue, F.-Z. Wang, X. Huang, B.-Q. Gong, Y. Tao, et al., Plasma membrane-nucleo-cytoplasmic coordination of a receptor-like cytoplasmic kinase promotes EDS1-dependent plant immunity, *Nat. Plants* 8 (2022) 802–816, <https://doi.org/10.1038/s41477-022-01195-x>.
- [135] K. Yamaguchi, Y. Yoshimura, S. Nakagawa, H. Mezaki, OSDRE2 contributes to chitin-triggered response through its interaction with OsRLCK185, *Biosci. Biotechnol. Biochem.* (2018), <https://doi.org/10.1080/09168451.2018.1543012>.
- [136] N. Maruta, Y. Trusov, A.M. Jones, J.R. Botella, Heterotrimeric G proteins in plants: canonical and atypical G α subunits, *Int. J. Mol. Sci.* 22 (11841) (2021), <https://doi.org/10.3390/ijms222111841>.
- [137] A. Akamatsu, H.L. Wong, M. Fujiwara, J. Okuda, K. Nishide, K. Uno, et al., An OsCEBIP/OsCERK1-OsRacGEF1-OsRac1 module is an essential early component of chitin-induced rice immunity, *Cell Host Microbe* 13 (4) (2013) 465–476, <https://doi.org/10.1016/j.chom.2013.03.007>.
- [138] Y. Zhao, Y. Shi, G. Jiang, Y. Wu, M. Ma, X. Zhang, et al., Rice extra-large G proteins play pivotal roles in controlling disease resistance and yield-related traits, *New Phytol.* 234 (2022) 607–617, <https://doi.org/10.1111/nph.17997>.
- [139] Y. Wang, H. Zhang, P. Wang, H. Zhong, W. Liu, S. Zhang, et al., Arabidopsis extra-large G protein 1 (XLG1) functions together with XLG2 and XLG3 in PAMP-triggered MAPK activation and immunity, *J. Integr. Plant Biol.* (2022), <https://doi.org/10.1111/jipb.13391>.
- [140] Z. Song, C. Zhang, L. Chen, P. Jin, C. Tetteh, X. Zhou, et al., The Arabidopsis small G-protein ATRAN1 is a positive regulator in chitin-induced stomatal closure and disease resistance, *Mol. Plant Pathol.* 22 (2021) 92–107, <https://doi.org/10.1111/mpp.13010>.
- [141] Y. Li, Q. Zhang, L. Gong, J. Kong, X. Wang, G. Xu, et al., Extra-large G proteins regulate disease resistance by directly coupling to immune receptors in *Nicotiana benthamiana*, *Phytopathol. Res.* 4 (49) (2022), <https://doi.org/10.1186/s42483-022-00155-9>.
- [142] B. Chen, Y. Zhang, J. Yang, M. Zhang, Q. Ma, X. Wang, et al., The G-protein a subunit GhGPA positively regulates *Gossypium hirsutum* resistance to *Verticillium dahliae* via induction of SA and JA signaling pathways and ROS accumulation, *Crop J* 9 (4) (2021) 823–833, <https://doi.org/10.1016/j.cj.2020.09.008>.
- [143] Y. Wang, Y. Wu, H. Zhong, S. Chen, K.-B. Wong, Y. Xia, Arabidopsis PUB2 and PUB4 connect signaling components of pattern-triggered immunity, *New Phytol.* 223 (2022) 2249–2265, <https://doi.org/10.1111/nph.17922>.
- [144] Y. Wang, Y. Wu, B. Yu, Z. Yin, Y. Xia, EXTRA-LARGE G proteins interact with E3 ligases PUB4 and PUB2 and function in cytokinin and developmental processes, *Plant Physiol.* 173 (2) (2017) 1235–1246, <https://doi.org/10.1104/pp.16.00816>.
- [145] K. Ishikawa, K. Yamaguchi, K. Sakamoto, S. Yoshimura, K. Inoue, S. Tsuge, et al., Bacterial effector modulation of host E3 ligase activity suppresses PAMP-triggered immunity in rice, *Nat. Commun.* 5 (5430) (2014), <https://doi.org/10.1038/ncomms6430>.
- [146] K. Ichimaru, K. Yamaguchi, K. Harada, Y. Nishio, M. Hori, K. Ishikawa, et al., Cooperative regulation of PBI1 and MAPKs controls WRKY45 transcription factor in rice immunity, *Nat. Commun.* 13 (2397) (2022), <https://doi.org/10.1038/s41467-022-30131-y>.
- [147] Z. Zhou, Y. Zhao, G. Bi, X. Liang, J. Zhou, Early signalling mechanisms underlying receptor kinase-mediated immunity in plants, *Phil. Trans. R. Soc. B* 374 (20180310) (2019), <https://doi.org/10.1098/rstb.2018.0310>.

- [148] W. Tian, C. Hou, Z. Ren, C. Wang, F. Zhao, D. Dahlbeck, et al., A calmodulin-gated calcium channel links pathogen patterns to plant immunity, *Nature* 572 (2019) 131–135, <https://doi.org/10.1038/s41586-019-1413-y>.
- [149] L. Navazio, R. Moscatello, D. Bellincampi, B. Baldan, F. Meggio, M. Brini, et al., The role of calcium in oligogalacturonide-activated signalling in soybean cells, *Planta* 215 (2002) 596–605, <https://doi.org/10.1007/s00425-002-0776-7>.
- [150] L. Zhao, Y. Chen, W. Yang, Y. Zhang, W. Chen, C. Feng, Polysaccharide peptide-induced virus resistance depends on Ca²⁺ influx by increasing the salicylic acid content and upregulating the leucine-rich repeat gene in *Arabidopsis thaliana*, *Mol. Plant Microbe Interact.* 31 (5) (2018) 516–524, <https://doi.org/10.1094/MPMI-10-17-0242-R>.
- [151] Y. Yang, L. Lu, D. Sun, J. Wang, N. Wang, L. Qiao, et al., Fungus polygalacturonase-generated oligogalacturonide restrains fruit softening in ripening tomato, *J. Agric. Food Chem.* 70 (3) (2022) 759–769, <https://doi.org/10.1021/acs.jafc.1c04972>.
- [152] M. Giovannoni, L. Marti, S. Ferrari, N. Tanaka-Takada, M. Maeshima, T. Ott, et al., The plasma membrane associated Ca²⁺-binding protein, PCaP1, is required for oligogalacturonide and flagellin-induced priming and immunity, *Plant Cell Environ.* 44 (2021) 3078–3093, <https://doi.org/10.1111/pce.14118>.
- [153] W. Pongprayoon, S. Maksud, N. Phaonakrop, J. Jaresithikunchai, U. Uwaisetwathana, A. Panya, et al., Phosphoproteome analysis reveals chitosan-induced resistance to osmotic stress in rice (*Oryza sativa* L.) seedlings, *J. Plant Interact.* 17 (1) (2022) 894–910, <https://doi.org/10.1080/17429145.2022.2114556>.
- [154] C. Huang, Y. Yan, H. Zhao, Y. Ye, Y. Cao, Arabidopsis CPK5 phosphorylates the chitin receptor LYK5 to regulate plant innate immunity, *Front. Plant Sci.* 11 (2020) 702, <https://doi.org/10.3389/fpls.2020.00702>.
- [155] M. Kato, T. Aoyama, M. Maeshima, The Ca²⁺ binding protein PCaP2 located on the plasma membrane is involved in root hair development as a possible signal transducer, *Plant J.* 74 (2013) 690–700, <https://doi.org/10.1111/tpj.12155>.
- [156] F. Takahashi, T. Mizoguchi, R. Yoshida, K. Ichimura, K. Shinozaki, Calmodulin-dependent activation of MAP kinase for ROS homeostasis in Arabidopsis, *Mol. Cell* 41 (6) (2011) 649–660, <https://doi.org/10.1016/j.molcel.2011.02.029>.
- [157] Y. He, J. Zhou, X. Meng, Phosphoregulation of Ca²⁺ influx in plant immunity, *Trends Plant Sci.* (2019), <https://doi.org/10.1016/j.tplants.2019.10.004>.
- [158] T. Guerra, S. Schilling, K. Hake, K. Gorzolka, F.P. Sylvester, B. Conrads, et al., Calcium-dependent protein kinase 5 links calcium signaling with N-hydroxy-l-pipecolic acid- and SARD1-dependent immune memory in systemic acquired resistance, *New Phytol.* 4 (2020), <https://doi.org/10.1111/nph.16147>.
- [159] P. Yuan, K. Tanaka, B.W. Poovaiyah, B.W. Poovaiyah, Calcium/calmodulin-mediated defense signaling: what is looming on the horizon for AtSR1/CAMTA3-mediated signaling in plant immunity, *Front. Plant Sci.* 12 (2022) 795353, <https://doi.org/10.3389/fpls.2021.795353>.
- [160] Y. Prodan, S. Munemasa, N.-E.-N. Nahar, Y. Nakamura, Y. Murata, Guard cell salicylic acid signaling is integrated into abscisic acid signaling via the Ca²⁺/CPK-dependent, *Plant Physiol.* 178 (2018) 441–450, <https://doi.org/10.1104/pp.18.00321>.
- [161] H. Huang, F. Ullah, D. Zhou, M. Yi, Y. Zhao, Mechanisms of ROS regulation of plant development and stress responses, *Front. Plant Sci.* 10 (2019) 800, <https://doi.org/10.3389/fpls.2019.00800>.
- [162] C. Hua, Y. Li, X. Wang, K. Kai, M. Su, D. Zhang, The effect of low and high molecular weight chitosan on the control of gray mold (*Botrytis cinerea*) on kiwifruit and host response, *Sci. Hortic.* 246 (2019) 700–709, <https://doi.org/10.1016/j.scienta.2018.11.038>.
- [163] R. Paulert, F. Brunel, R.L.J. Melcher, S. Cord-landwehr, A. Niehues, M. Mormann, et al., The non-sulfated ulvanobiuronic acid of ulvans is the smallest active unit able to induce an oxidative burst in dicot cells, *Carbohydr. Polym.* 270 (2021), <https://doi.org/10.1016/j.carbpol.2021.118338>.
- [164] A. Aziz, B. Poinssot, X. Daire, M. Adrian, A. Bézier, B. Lambert, et al., Laminarin elicits defense responses in grapevine and induces protection against *Botrytis cinerea* and *Plasmopara viticola*, *Mol. Plant Microbe Interact.* 16 (12) (2003) 1118–1128, <https://doi.org/10.1094/MPMI.2003.16.12.1118>.
- [165] A. Aziz, A. Heyraud, B. Lambert, Oligogalacturonide signal transduction, induction of defense-related responses and protection of grapevine against *Botrytis cinerea*, *Planta* 218 (2004) 767–774, <https://doi.org/10.1007/s00425-003-1153-x>.
- [166] E. Gubaeva, A. Gubaev, R.L.J. Melcher, S. Cord-landwehr, R. Singh, N. Eddine, et al., ‘Slipped sandwich’ model for chitin and chitosan perception in Arabidopsis, *Mol. Plant Microbe Interact.* 31 (11) (2018) 1145–1153, <https://doi.org/10.1094/MPMI-04-18-0098-R>.
- [167] M.B. de Freitas, M.J. Stadnik, Ulvan-induced resistance in *Arabidopsis thaliana* against *Alternaria brassicicola* requires reactive oxygen species derived from NADPH oxidase, *Physiol. Mol. Plant Pathol.* 90 (2015) 49–56, <https://doi.org/10.1016/j.pmpp.2015.03.002>.
- [168] Y. Li, S. Xu, J. Gao, S. Pan, G. Wang, Glucose- and mannose-induced stomatal closure is mediated by ROS production, Ca²⁺ and water channel in *Vicia faba*, *Physiol. Plant.* 156 (2016) 252–261, <https://doi.org/10.1111/pp.12353>.
- [169] Y. Kadota, J. Sklenar, P. Derbyshire, L. Stransfeld, S. Asai, V. Ntoukakis, et al., Direct regulation of the NADPH oxidase RBOHD by the PRR-associated kinase BIK1 during plant immunity, *Mol. Cell* 54 (1) (2014) 43–55, <https://doi.org/10.1016/j.molcel.2014.02.021>.
- [170] T. Lukan, M. Pompe-Novak, Š. Baebler, M. Tušek-Znidarič, A. Kladnik, M. Kržižnik, et al., Spatial accumulation of salicylic acid is in effector-triggered immunity of potato against viruses regulated by RBOHD, *bioRxiv* (2020), <https://doi.org/10.1101/2020.01.06.889998>.
- [171] V. Stanley-Raja, S. Senthil-Nathan, K.M.P. Chanthini, H. Sivanesh, R. Ramasubramanian, S. Karthi, et al., Biological activity of chitosan inducing resistance efficiency of rice (*Oryza sativa* L.) after treatment with fungal based chitosan, *Sc. Rep* 11 (2021) 20488, <https://doi.org/10.1038/s41598-021-99391-w>.
- [172] N. Rendina, M. Nuzzaci, A. Scopa, A. Cuyppers, A. Sofo, Chitosan-elicited defense responses in *Cucumber mosaic virus* (CMV)-infected tomato plants, *J. Plant Physiol.* 234–235 (2019) 9–17, <https://doi.org/10.1016/j.jplph.2019.01.003>.
- [173] M.N. da Silva, C.S. Santos, A. Cruz, A. López-Villamor, M.W. Vasconcelos, Chitosan increases *Pinus pinaster* tolerance to the pinewood nematode (*Bursaphelenchus xylophilus*) by promoting plant antioxidative metabolism, *Sc. Rep* 11 (2021) 3781, <https://doi.org/10.1038/s41598-021-83445-0>.
- [174] X. Wang, K. Zheng, W. Cheng, J. Li, X. Liang, J. Shen, et al., Field application of star polymer-delivered chitosan to amplify plant defense against potato late blight, *Chem. Eng. J.* 417 (2021) 129327, <https://doi.org/10.1016/j.cej.2021.129327>.
- [175] Z. Fan, Y. Qin, S. Liu, R. Xing, H. Yu, P. Li, Chitosan oligosaccharide fluorinated derivative control root-knot nematode (*Meloidogyne incognita*) disease based on the multi-efficacy strategy, *Mar. Drugs* 18 (273) (2020), <https://doi.org/10.3390/md18050273>.
- [176] R.R. Singh, B. Chinnasri, L. De Smet, A. Haec, K. Demeestere, P. Van Cutsem, et al., Systemic defense activation by COS-OGA in rice against root-knot nematodes depends on stimulation of the phenylpropanoid pathway, *Plant Physiol. Biochem.* 142 (2019) 202–210, <https://doi.org/10.1016/j.plaphy.2019.07.003>.
- [177] Y. Bektas, FytoSol, a promising plant defense elicitor, controls early blight (*Alternaria solani*) disease in the tomato by inducing host resistance-associated gene expression, *Horticulturae* 8 (484) (2022), <https://doi.org/10.3390/horticulturae8060484>.
- [178] P.F. Zhao, S.Q. Wang, Z.L. Xu, M. De Liao, Tobacco-acquired resistance induced by an exopolysaccharide of *Paenibacillus kribbensis* PS04 against bacterial wilt, *Biocont. Sci. Technol.* (2020), <https://doi.org/10.1080/09583157.2020.1713298>.
- [179] S. Bouissil, C. Guérin, J. Roche, P. Dubessay, Z. El Alaoui-Talibi, G. Pierre, et al., Induction of defense gene expression and the resistance of date palm to *Fusarium oxysporum* f. sp. *Albedinis* in response to alginate extracted from *Bifurcaria bifurcata*, *Mar. Drugs* 20 (88) (2022), <https://doi.org/10.3390/md20020088>.
- [180] C. Zhang, P. Howlader, T. Liu, X. Sun, X. Jia, Alginate oligosaccharide (AOS) induced resistance to Pst DC3000 via salicylic acid-mediated signaling pathway in *Arabidopsis thaliana*, *Carbohydr. Polym.* 225 (2019), <https://doi.org/10.1016/j.carbpol.2019.115221>.
- [181] S. Pettongkhao, A. Bilanglod, K. Khompatara, N. Churngchow, Sulphated polysaccharide from *Acanthophora spicifera* induced *Hevea brasiliensis* defense responses against *Phytophthora palmivora* infection, *Plants* 8 (73) (2019), <https://doi.org/10.3390/plants8030073>.
- [182] M.C. de Borba, A.C. Velho, A. Maia-grondard, R. Baltenweck, M. Magnin-robot, B. Randoux, et al., The algal polysaccharide ulvan induces resistance in wheat against *Zymoseptoria tritici* without major alteration of leaf metabolism, *Front. Plant Sci.* 12 (2021) 703712, <https://doi.org/10.3389/fpls.2021.703712>.
- [183] M. Pugliese, M. Monchiero, M. Lodovica, A. Garibaldi, M. Pugliese, Application of laminarin and calcium oxide for the control of grape powdery mildew on *Vitis vinifera* cv. *Moscato*, *J. Plant Dis. Prot.* 8 (2018), <https://doi.org/10.1007/s41348-018-0162-8>.
- [184] P. Howlader, S. Kumar, X. Jia, C. Zhang, W. Wang, H. Yin, Oligogalacturonides induce resistance in *Arabidopsis thaliana* by triggering salicylic acid and jasmonic acid pathways against Pst DC3000, *Int. J. Biol. Macromol.* 164 (2020) 4054–4064, <https://doi.org/10.1016/j.ijbiomac.2020.09.026>.
- [185] C. Silva-Sanzana, D. Zavala, F. Moraga, A. Herrera-Vásquez, F. Blanco-Herrera, Oligogalacturonides enhance resistance against aphids through pattern-triggered immunity and activation of salicylic acid signaling, *Int. J. Mol. Sci.* 23 (9753) (2022), <https://doi.org/10.3390/ijms23179753>.

- [186] C. Zhao, C. Wu, K. Li, J.F. Kennedy, M. Wisniewski, L. Gao, et al., Effect of oligogalacturonides on seed germination and disease resistance of sugar beet seedling and root, *J. Fungi* 8 (716) (2022), <https://doi.org/10.3390/jof8070716>.
- [187] M. Versluis and W. Van den Ende, Sweet immunity aspects during levan oligosaccharide-mediated priming in rocket against *Botrytis cinerea*, *Biomolecules* 12 (370) 202, <https://doi.org/10.3390/biom12030370>.
- [188] H.C.J. van Rensburg, Z. Takács, F. Freynschlag, E.T. Öner, C. Jonak, W. Van den Ende, Fructans prime ROS dynamics and *Botrytis cinerea* resistance in *Arabidopsis*, *Antioxidants* 9 (805) (2020), <https://doi.org/10.3390/antiox9090805>.
- [189] M. Versluis, E. Toksoy Öner, W. Van Den Ende, Fructan oligosaccharide priming alters apoplastic sugar dynamics and improves resistance against *Botrytis cinerea* in chicory, *J. Exp. Bot.* 73 (12) (2022) 4214–4235, <https://doi.org/10.1093/jxb/erac140>.
- [190] A. Svara, L.P. Tarkowski, H.C.J. van Rensburg, E. Deleye, J. Vaerten, N. De Storme, et al., Sweet immunity: the effect of exogenous fructans on the susceptibility of apple (*Malus × domestica* Borkh.) to *Venturia inaequalis*, *Int. J. Mol. Sci.* 21 (5885) (2020), <https://doi.org/10.3390/ijms21165885>.
- [191] L.P. Tarkowski, B. Van de Poel, M. Höfte, W. Van den Ende, Sweet immunity: inulin boosts resistance of lettuce (*Lactuca sativa*) against grey mold (*Botrytis cinerea*) in an ethylene-dependent manner, *Int. J. Mol. Sci.* 20 (1052) (2019), <https://doi.org/10.3390/ijms20051052>.
- [192] S. Pring, H. Kato, S. Imano, M. Camagna, A. Tanaka, H. Kimoto, et al., Induction of plant disease resistance by mixed oligosaccharide elicitors prepared from plant cell wall and crustacean shells, *Physiol. Plant.* 175(5), e14052, <https://doi.org/10.1111/pp1.14052>.
- [193] H. Turk, Chitosan-induced enhanced expression and activation of alternative oxidase confer tolerance to salt stress in maize seedlings, *Plant Physiol. Biochem.* 141 (2019) 415–422, <https://doi.org/10.1016/j.plaphy.2019.06.025>.
- [194] G. Zhang, Y. Wang, K. Wu, Q. Zhang, Y. Feng, Y. Miao, et al., Exogenous application of chitosan alleviate salinity stress in lettuce (*Lactuca sativa* L.), *Horticulturae* 7 (342) (2021), <https://doi.org/10.3390/horticulturae7100342>.
- [195] R.G. Ávila, P.C. Magalhães, L.C. Vitorino, L.A. Bessa, K.R.D. de Souza, R.B. Queiroz, et al., Chitosan induces sorghum tolerance to water deficits by positively regulating photosynthesis and the production of primary metabolites, osmoregulators, and antioxidants, *J. Soil Sci. Plant Nutr.* 23 (2023) 1156–1172, <https://doi.org/10.1007/s42729-022-01111-4>.
- [196] Y. Zhang, L. Fan, M. Zhao, Q. Chen, Z. Qin, Z. Feng, et al., Chitoooligosaccharide plays essential roles in regulating proline metabolism and cold stress tolerance in rice seedlings, *Acta Physiol. Plant.* 41 (77) (2019), <https://doi.org/10.1007/s11738-019-2864-3>.
- [197] S.A. Dowom, Z. Karimian, M.M. Dehnavi, L. Samiei, Chitosan nanoparticles improve physiological and biochemical responses of *Salvia abrotanoides* (Kar.) under drought stress, *BMC Plant Biol.* 22 (364) (2022), <https://doi.org/10.1186/s12870-022-03689-4>.
- [198] D. Zhao, T. Li, Z. Hao, M. Cheng, J. Tao, Exogenous trehalose confers high temperature stress tolerance to herbaceous peony by enhancing antioxidant systems, activating photosynthesis, and protecting cell structure, *Cell Stress Chaperones* 24 (2019) 247–257, <https://doi.org/10.1007/s12192-018-00961-1>.
- [199] M.S. Sadak, H.M.S. El-bassiouny, M.G. Dawood, Role of trehalose on antioxidant defense system and some osmolytes of quinoa plants under water deficit, *Bull. Natl. Res. Cent.* 43 (5) (2019), <https://doi.org/10.1186/s42269-018-0039-9>.
- [200] Y. Yang, Y. Yao, J. Li, J. Zhang, X. Zhang, L. Hu, et al., Trehalose alleviated salt stress in tomato by regulating ROS metabolism, photosynthesis, osmolyte synthesis, and trehalose metabolic pathways, *Front. Plant Sci.* 13 (2022) 772948, <https://doi.org/10.3389/fpls.2022.772948>.
- [201] M. Shahbaz, A. Abid, A. Masood, E.A. Waraich, Foliar-applied trehalose modulates growth, mineral nutrition, photosynthetic ability, and oxidative defense system of rice (*Oryza sativa* L.) under saline stress, *J. Plant Nutr.* 40 (4) (2017) 584–599, <https://doi.org/10.1080/1094167.2016.1263319>.
- [202] A. El Amrani, I. Couée, R. Berthomé, F. Ramel, G. Gouesbet, C. Sulmon, Involvement of polyamines in sucrose-induced tolerance to atrazine-mediated chemical stress in *Arabidopsis thaliana*, *J. Plant Physiol.* 238 (2019) 1–11, <https://doi.org/10.1016/j.jplph.2019.04.012>.
- [203] P. Zou, X. Lu, H. Zhao, Y. Yuan, L. Meng, C. Zhang, Polysaccharides derived from the brown algae *Lessonia nigrescens* enhance salt stress tolerance to wheat seedlings by enhancing the antioxidant system and modulating intracellular ion concentration, *Front. Plant Sci.* 10 (2019) 48, <https://doi.org/10.3389/fpls.2019.00048>.
- [204] Y. Ma, H. Jie, L. Zhao, Y. Zhang, P. He, X. Lv, et al., Exogenous xyloglucan oligosaccharides alleviate cadmium toxicity in *Boehmeria nivea* by increasing the cadmium fixation capacity of cell walls, *Agronomy* 13 (2023) 2786, <https://doi.org/10.3390/agronomy13112786>.
- [205] Y. Wang, Y. Wu, H. Zhang, P. Wang, Y. Xia, Arabidopsis MAPKK kinases YODA, MAPKKK3, and MAPKKK5 are functionally redundant in development and immunity, *Plant Physiol.* 190 (2022) 206–210, <https://doi.org/10.1093/plphys/kiac270>.
- [206] N. Li, X. Han, D. Feng, D. Yuan, L. Huang, Signaling crosstalk between salicylic acid and ethylene/jasmonate in plant defense: do we understand what they are whispering? *Int. J. Mol. Sci.* 20 (671) (2019) <https://doi.org/10.3390/ijms20030671>.
- [207] N. Aerts, M.P. Mendes, S.C.M. Van Wees, Multiple levels of crosstalk in hormone networks regulating plant defense, *Plant J.* 105 (2021) 489–504, <https://doi.org/10.1111/tj.15124>.
- [208] X. Jia, Q. Meng, H. Zeng, W. Wang, H. Yin, Chitosan oligosaccharide induces resistance to *Tobacco mosaic virus* in *Arabidopsis* via the salicylic acid-mediated signalling pathway, *Sci. Rep.* 6 (2016), <https://doi.org/10.1038/srep26144>.
- [209] D. de Vega, N. Holden, P.E. Hedley, J. Morris, E. Luna, A. Newton, Chitosan primes plant defence mechanisms against *Botrytis cinerea*, including expression of Avr9/Cf-9 rapidly-elicited genes, *Plant Cell Environ.* 44 (2021) 290–303, <https://doi.org/10.1111/pce.13921>.
- [210] G. van Aubel, P. Cambie, M. Dieu, P. van Cutsem, Plant immunity induced by COS-OGA elicitor is a cumulative process that involves salicylic acid, *Plant Sci.* 247 (2016) 60–70, <https://doi.org/10.1016/j.plantsci.2016.03.005>.
- [211] G. van Aubel, S. Serderidis, J. Ivens, A. Clinckemillie, A. Legrève, B. Hause, et al., Oligosaccharides successfully thwart hijacking of the salicylic acid pathway by *Phytophthora infestans* in potato leaves, *Plant Pathol.* 67 (9) (2018) 1901–1911, <https://doi.org/10.1111/ppa.12908>.
- [212] Y. Wu, D. Zhang, J.Y. Chu, P. Boyle, Y. Wang, I.D. Brindle, et al., The Arabidopsis NPR1 protein is a receptor for the plant defense hormone salicylic acid, *Cell Rep.* 1 (2012) 639–647, <https://doi.org/10.1016/j.celrep.2012.05.008>.
- [213] Y. Prodhon, M. Issak, S. Munemasa, Y. Murata, Salicylic acid receptor NPR1 is involved in guard cell chitosan signaling, *Biosci. Biotechnol. Biochem.* (2020), <https://doi.org/10.1080/09168451.2020.1718485>.
- [214] J.S. Patel, V. Selvaraj, L.R. Gunupuru, P.K. Rathor, B. Prithiviraj, Combined application of *Ascophyllum nodosum* extract and chitosan synergistically activates host-defense of peas against powdery mildew, *BMC Plant Biol.* 20 (113) (2020), <https://doi.org/10.1186/s12870-020-2287-8>.
- [215] P. Geng, S. Zhang, J. Liu, C. Zhao, J. Wu, Y. Cao, et al., MYB20, MYB42, MYB43, and MYB85 regulate phenylalanine and lignin biosynthesis during secondary cell wall formation, *Plant Physiol.* 182 (2020) 1272–1283, <https://doi.org/10.1104/pp.19.01070>.
- [216] Q.-M. Gao, S. Venugopal, D. Navarre, A. Kachroo, Low oleic acid-derived repression of jasmonic Acid-inducible defense responses requires the WRKY50 and WRKY51 proteins, *Plant Physiol.* 155 (2011) 464–476, <https://doi.org/10.1104/pp.110.166876>.
- [217] Y. Hou, Y. Wang, L. Tang, X. Tong, L. Wang, L. Liu, et al., SAPK10-mediated phosphorylation on WRKY72 releases its suppression on jasmonic acid biosynthesis and bacterial blight resistance, *iScience* 16 (2019) 499–510, <https://doi.org/10.1016/j.isci.2019.06.009>.
- [218] L.T. Phuong, L. Zhao, A.N. Fitrianti, H. Matsui, Y. Noutoshi, M. Yamamoto, et al., The plant activator saccharin induces resistance to wheat powdery mildew by activating multiple defense-related genes, *J. Gen. Plant Pathol.* (2019), <https://doi.org/10.1007/s10327-019-00900-7>.
- [219] X. Chen, C. Li, H. Wang, Z. Guo, WRKY transcription factors: evolution, binding, and action, *Phytopathol. Res.* 1 (13) (2019), <https://doi.org/10.1186/s42483-019-0022-x>.
- [220] E. Samari, M. Sharifi, F. Ghanati, E. Fuss, N. Ahmadian, L. Lariciresinol, et al., Chitosan-induced Phenolics Production Is Mediated by Nitrogenous Regulatory Molecules: NO and PAs in *Linum Album* Hairy Roots, *PCTOC*, 2020, <https://doi.org/10.1007/s11240-019-01753-w>.
- [221] H.C. Janse van Rensburg, A.M. Limami, W. Van den Ende, Spermine and spermidine priming against *Botrytis cinerea* modulates ROS dynamics and metabolism in *Arabidopsis*, *Biomolecules* 11 (223) (2021), <https://doi.org/10.3390/biom11020223>.
- [222] I. Ben Salah, S. Aghrouss, A. Douira, S. Aissam, Z. El Alaoui-Talibi, A. Filali-Maltouf, C. El Modafar, Seaweed polysaccharides as bio-elicitors of natural defenses in olive trees against verticillium wilt of olive, *J. Plant Interact.* 13 (1) (2018) 248–255, <https://doi.org/10.1080/17429145.2018.1471528>.
- [223] G. Le Mire, A. Siah, B. Marolleau, M. Gaucher, C. Maumen, Y. Brostaux, et al., Evaluation of λ -carrageenan, CpG-ODN, glycine betaine, spirulina platensis, and ergosterol as elicitors for control of *Zymoseptoria tritici* in wheat, *Phytopathology* 109 (3) (2019) 409–417, <https://doi.org/10.1094/PHYTO-11-17-0367-R>.

- [224] L. Kappel, N. Kosa, S. Gruber, The multilateral efficacy of chitosan and trichoderma on sugar beet, *J. Fungi* 137 (2022), <https://doi.org/10.3390/jof8020137>, 6.
- [225] F. Zhu, M.-Y. Cao, Q.-P. Zhang, R. Mohan, J. Schar, M. Michaela et al., Join the green team: Inducers of plant immunity in the plant disease sustainable control toolbox, *J. Adv. Res.* <https://doi.org/10.1016/j.jare.2023.04.016>.
- [226] L.R. Gunupuru, J.S. Patel, M.W. Sumarah, J.B. Renaud, E.G. Mantin, B. Prithiviraj, A plant biostimulant made from the marine brown algae *Ascophyllum nodosum* and chitosan reduce *Fusarium* head blight and mycotoxin contamination in wheat, *PLoS One* 14 (9) (2019) e0220562, <https://doi.org/10.1371/journal.pone.0220562>.
- [227] K. Narula, E. Elagamey, M.A.E. Abdellatif, A. Sinha, S. Ghosh, N. Chakraborty, et al., Chitosan-triggered immunity to *Fusarium* in chickpea is associated with changes in the plant extracellular matrix architecture, stomatal closure and remodeling of the plant metabolome and proteome, *Plant J.* 103 (2) (2020) 14750, <https://doi.org/10.1111/tpj.14750>.
- [228] M.C. de Borba, A.C. Velho, M.B. de Freitas, M. Holvoet, A. Maia-Grondard, R. Baltenweck, et al., A laminarin-based formulation protects wheat against *Zymoseptoria tritici* via direct antifungal activity and elicitation of host defense-related genes, *Plant Dis.* 106 (5) (2022), <https://doi.org/10.1094/PDIS-08-21-1675-RE>.
- [229] Y. Saijo, E.P. Loo, Plant immunity in signal integration between biotic and abiotic stress responses, *New Phytol.* 225 (2020) 87–104, <https://doi.org/10.1111/nph.15989>.
- [230] Z. Czékus, P. Poór, I. Tari, A. Ördög, Effects of light and daytime on the regulation of chitosan-induced stomatal responses and defence in tomato plants, *Plants* 9 (59) (2020), <https://doi.org/10.3390/plants9010059>.
- [231] Z. Czékus, N. Iqbal, B. Pollák, A. Martics, A. Ördög, P. Poór, Role of ethylene and light in chitosan-induced local and systemic defence responses of tomato plants, *J. Plant Physiol.* 263 (2021) 153461, <https://doi.org/10.1016/j.jplph.2021.153461>.
- [232] Y. Liang, K. Toth, Y. Cao, K. Tanaka, C. Espinoza, G. Stacey, Lipochitooligosaccharide recognition: an ancient story, *New Phytol.* 204 (2014) 289–296, <https://doi.org/10.1111/nph.12898>.
- [233] C. Zipfel, G.E.D. Oldroyd, Plant signalling in symbiosis and immunity, *Nature* 543 (2017) 328–336, <https://doi.org/10.1038/nature22009>.
- [234] Y. Liang, Y. Cao, K. Tanaka, S. Thibivilliers, J. Wan, J. Choi, et al., Nonlegumes respond to rhizobial nod factors by suppressing the innate immune response, *Science* (1979) (2013), <https://doi.org/10.1126/science.1242736>.
- [235] A. Nars, C. Lafitte, M. Chabaud, S. Drouillard, H. Méliida, S. Danoun, et al., *Aphanomyces euteiches* cell wall fractions containing novel glucan-chitosaccharides induce defense genes and nuclear calcium oscillations in the plant host *Medicago truncatula*, *PLoS One* 8 (9) (2013), <https://doi.org/10.1371/journal.pone.0075039>.
- [236] T.A. Rush, V. Puech-pagès, A. Bascaules, P. Jargeat, F. Maillet, A. Haouy, et al., Lipo-chitooligosaccharides as regulatory signals of fungal growth and development, *Nat. Commun.* 11 (3897) (2020), <https://doi.org/10.1038/s41467-020-17615-5>.
- [237] F. Maillet, V. Poinso, O. André, V. Puech-Pagès, A. Haouy, M. Gueunier, et al., Fungal lipochitooligosaccharide symbiotic signals in *Arbuscular mycorrhiza*, *Nature* 469 (2011), <https://doi.org/10.1038/nature09622>.
- [238] A. Genre, M. Chabaud, C. Balzerque, V. Puech-Pages, M. Novero, T. Rey, et al., Short-chain chitin oligomers from arbuscular mycorrhizal fungi trigger nuclear Ca²⁺ spiking in *Medicago truncatula* roots and their production is enhanced by strigolactone, *New Phytol.* 198 (2013) 179–189, <https://doi.org/10.1111/nph.12146>.
- [239] G. Carotenuto, M. Chabaud, K. Miyata, M. Capozzi, N. Takeda, H. Kaku, et al., The rice LysM receptor-like kinase OsCERK1 is required for the perception of short-chain chitin oligomers in arbuscular mycorrhizal signaling, *New Phytol.* 214 (2017) 1440–1446, <https://doi.org/10.1111/nph.14539>.
- [240] V. Volpe, G. Carotenuto, C. Berzoro, L. Cagnina, V. Puech-Pagès, A. Genre, Short chain chito-oligosaccharides promote arbuscular mycorrhizal colonization in *Medicago truncatula*, *Carbohydr. Polym.* 229 (2020), <https://doi.org/10.1016/j.carbpol.2019.115505>.
- [241] J. Sun, J.B. Miller, E. Granqvist, A. Wiley-Kalil, E. Gobatto, F. Maillet, et al., Activation of symbiosis signaling by arbuscular mycorrhizal fungi in legumes and rice, *Plant Cell* 27 (2015) 823–838, <https://doi.org/10.1105/tpc.114.131326>.
- [242] X.-R. Li, J. Sun, D. Albinsky, D. Zarrabian, R. Hull, T. Lee, et al., Nutrient regulation of lipochitooligo-saccharide recognition in plants via NSP1 and NSP2, *Nat. Commun.* 13 (6421) (2022), <https://doi.org/10.1038/s41467-022-33908-3>.
- [243] A. Miya, P. Albert, T. Shinya, Y. Desaki, K. Ichimura, K. Shirasu, et al., CERK1, a LysM receptor kinase, is essential for chitin elicitor signaling in Arabidopsis, *Proc. Natl. Acad. Sci. U.S.A.* 104 (49) (2007) 19613–19618, <https://doi.org/10.1073/pnas.0705147104>.
- [244] J. He, C. Zhang, H. Dai, H. Liu, X. Zhang, J. Yang, et al., A LysM receptor heteromer mediates perception of arbuscular mycorrhizal symbiotic signal in rice, *Mol. Plant* 12 (2019) 1561–1576, <https://doi.org/10.1016/j.molp.2019.10.015>.
- [245] F. Feng, J. Sun, G. V Radhakrishnan, T. Lee, Z. Bozsóki, S. Fort, et al., A combination of chitooligosaccharide and lipochitooligosaccharide recognition promotes arbuscular mycorrhizal associations in *Medicago truncatula*, *Nat. Commun.* 10 (5047) (2019), <https://doi.org/10.1038/s41467-019-12999-5>.
- [246] S. Radutoiu, L.H. Madsen, E.B. Madsen, H.H. Felle, Y. Umehara, M. Grönlund, et al., Plant recognition of symbiotic bacteria requires two LysM receptor-like kinases, *Nature* 425 (2003) 585–592, <https://doi.org/10.1038/nature02039>.
- [247] P. Smit, E. Limpens, R. Geurts, E. Fedorova, E. Dolgikh, C. Gough, et al., *Medicago* LYK3, an entry receptor in rhizobial nodulation factor signaling, *Plant Physiol.* 145 (2007) 183–191, <https://doi.org/10.1104/pp.107.100495>.
- [248] A. Broghammer, L. Krusel, M. Blaise, J. Sauer, J.T. Sullivan, N. Maolanon, et al., Legume receptors perceive the rhizobial lipochitin oligosaccharide signal molecules by direct binding, *Proc. Natl. Acad. Sci. U.S.A.* 109 (34) (2012) 13859–13864, <https://doi.org/10.1073/pnas.1205171109>.
- [249] E. Murakami, J. Cheng, K. Gysel, Z. Bozsóki, Y. Kawaharada, C.T. Hjuler, et al., Epidermal LysM receptor ensures robust symbiotic signalling in *Lotus japonicus*, *Elife* 7 (2018), <https://doi.org/10.7554/eLife.33506>.
- [250] Y. Desaki, K. Miyata, M. Suzuki, N. Shibuya, H. Kaku, Plant immunity and symbiosis signaling mediated by LysM receptors, *Innate Immun.* 24 (2) (2018) 92–100, <https://doi.org/10.1177/1753425917738885>.
- [251] R. Op den Camp, A. Streng, S. De Mita, Q. Cao, E. Polone, W. Liu, et al., LysM-type mycorrhizal receptor recruited for rhizobium symbiosis in nonlegume *Parasponia*, *Science* 331 (909) (2011), <https://doi.org/10.1126/science.1198181>.
- [252] L. Buendía, T. Wang, A. Girardin, B. Lefebvre, The LysM receptor-like kinase SLYK10 regulates the arbuscular mycorrhizal symbiosis in tomato, *New Phytol.* 210 (2016) 184–195, <https://doi.org/10.1111/nph.13753>.
- [253] K. Miyata, T. Kozaki, Y. Kouzai, K. Ozawa, K. Ishii, E. Asamizu, et al., The bifunctional plant receptor, OsCERK1, regulates both chitin-triggered immunity and arbuscular mycorrhizal symbiosis in rice, *Plant Cell Physiol.* 55 (11) (2014) 1864–1872, <https://doi.org/10.1093/pcp/pcu129>.
- [254] X. Zhang, W. Dong, J. Sun, F. Feng, Y. Deng, Z. He, et al., The receptor kinase CERK1 has dual functions in symbiosis and immunity signalling, *Plant J.* 81 (2015) 258–267, <https://doi.org/10.1111/tpj.12723>.
- [255] K. Miyata, M. Hayafune, Y. Kobae, H. Kaku, Y. Nishizawa, Y. Masuda, et al., Evaluation of the role of the LysM receptor-like kinase, OsNFR5/OrSLK2 for AM symbiosis in rice, *Plant Cell Physiol.* 57 (2016) 2283–2290, <https://doi.org/10.1093/pcp/pcw144>.
- [256] W. Fuechtbauer, T. Yunusov, S. Schornack, S. Radutoiu, LYS12 LysM receptor decelerates *Phytophthora palmivora* disease progression in *Lotus japonicus*, *Plant J.* 93 (2018) 297–310, <https://doi.org/10.1111/tpj.13785>.
- [257] C. Gibelin-Viala, E. Amblard, V. Puech-Pages, M. Bonhomme, M. Garcia, Bascaules- A. Bedin, et al., The *Medicago truncatula* LysM receptor-like kinase LYK9 plays a dual role in immunity and the arbuscular mycorrhizal symbiosis, *New Phytol.* 223 (2019) 1516–1529, <https://doi.org/10.1111/nph.15891>.
- [258] C. Zhang, J. He, H. Dai, G. Wang, X. Zhang, C. Wang, et al., Discriminating symbiosis and immunity signals by receptor competition in rice, *Pro. Nat Aca Sci. USA* 118 (16) (2021), <https://doi.org/10.1073/pnas.2023738118>.
- [259] Z. Bozsóki, K. Gysel, S.B. Hansen, D. Lironi, C. Krönauer, F. Feng, et al., Ligand-recognizing motifs in plant LysM receptors are major determinants of specificity, *Science* 369 (6504) (2020) 663–670, <https://doi.org/10.1126/science.abb3377>.
- [260] T. Nakagawa, H. Kaku, Y. Shimoda, A. Sugiyama, M. Shimamura, K. Takanashi, From defense to symbiosis: limited alterations in the kinase domain of LysM receptor-like kinases are crucial for evolution of legume-rhizobium symbiosis, *Plant J.* 65 (2011) 169–180, <https://doi.org/10.1111/j.1365-313X.2010.04411.x>.

- [261] M. Suzuki, R. Numazaki, T. Nakagawa, N. Shibuya, H. Kaku, Cytoplasmic interaction of LysM receptors contributes to the formation of symbiotic receptor complex, *Plant Biotechnol.* 37 (2020), <https://doi.org/10.5511/plantbiotechnology.20.0511a>.
- [262] A. Aziz, A. Gauthier, A. Bézier, B. Poinssot, J.M. Joubert, A. Pugin, et al., Elicitor and resistance-inducing activities of β -1,4 cellooligosaccharides in grapevine, comparison with β -1,3 glucans and α -1,4 oligogalacturonides, *J. Exp. Bot.* 58 (6) (2007) 1463–1472, <https://doi.org/10.1093/jxb/erm008>.
- [263] S. Belchí-Navarro, L. Almagro, A.B. Sabater-Jara, F. Fernández-pérez, R. Bru, M.A. Pedreño, Early signaling events in grapevine cells elicited with cyclodextrins and methyl jasmonate, *Plant Physiol. Biochem.* 62 (2013) 107–110, <https://doi.org/10.1016/j.plaphy.2012.11.001>.
- [264] V. Escudero, L. Jordá, S. Sopena-Torres, H. Mérida, E. Miedes, A. Muñoz-Barrios, et al., Alteration of cell wall xylan acetylation triggers defense responses that counterbalance the immune deficiencies of plants impaired in the β -subunit of the heterotrimeric G-protein, *Plant J.* 92 (2017) 386–399, <https://doi.org/10.1111/tpj.13660>.
- [265] M. Zarattini, M. Corso, M.A. Kadowaki, A. Monclaro, S. Magri, I. Milanese, et al., LPMO-oxidized cellulose oligosaccharides evoke immunity in Arabidopsis conferring resistance towards necrotrophic fungus *B. cinerea*, *Commun. Biol.* 4 (727) (2021), <https://doi.org/10.1038/s42003-021-02226-7>.
- [266] F. Locci, M. Benedetti, D. Pontiggia, M. Citterico, C. Caprari, B. Mattei, et al., An Arabidopsis berberine bridge enzyme-like protein specifically oxidizes cellulose cellulose oligomers and plays a role in immunity, *Plant J.* 98 (2019) 540–554, <https://doi.org/10.1111/tpj.14237>.
- [267] S.H. Doares, T. Syrovstet, E.W. Weillert, C.A. Ryan, Oligogalacturonides and chitosan activate plant defensive genes through the octadecanoid pathway, *Proc. Natl. Acad. Sci. USA* 92 (1995) 4095–4098, <https://doi.org/10.1073/pnas.92.10.4095>.
- [268] S. Selim, J. Sanssené, S. Rossard, J. Courtois, Systemic induction of the defensin and phytoalexin pisatin pathways in pea (*Pisum sativum*) against *Aphanomyces euteiches* by acetylated and nonacetylated oligogalacturonides, *Molecules* 22 (2017) 1017, <https://doi.org/10.3390/molecules22061017>.
- [269] J. Messiaen, P. van Cutsem, Defense gene transcription in carrot cells treated with oligogalacturonides, *Plant Cell Physiol.* 34 (7) (1993) 78526, <https://doi.org/10.1093/oxfordjournals.pcp.a078526>.
- [270] P. Raymond, S. Grünberger, K. Paul, M. Müller, E.E. Farmer, Oligogalacturonide defense signals in plants: large fragments interact with the plasma membrane in vitro, *Proc. Natl. Acad. Sci. USA* 92 (1995) 4145–4149, <https://doi.org/10.1073/pnas.92.10.4145>.
- [271] S. Ferrari, R. Galletti, C. Denoux, G. De Lorenzo, F.M. Ausubel, J. Dewdney, Resistance to *Botrytis cinerea* induced in Arabidopsis by elicitors is independent of salicylic acid, ethylene, or jasmonate signaling but requires phytoalexin deficient 3, *Plant Physiol.* 144 (2007) 367–379, <https://doi.org/10.1104/pp.107.095596>.
- [272] S.D. Simpson, D.A. Ashford, D.J. Harvey, D.J. Bowles, Short chain oligogalacturonides induce ethylene production and expression of the gene encoding aminocyclopropane 1-carboxylic acid oxidase in tomato plants, *Glycobiology* 8 (6) (1998) 579–583, <https://doi.org/10.1093/glycob/8.6.579>.
- [273] M. Benedetti, I. Verrascina, D. Pontiggia, F. Locci, B. Mattei, G. De Lorenzo, et al., Four Arabidopsis berberine bridge enzyme-like proteins are specific oxidases that inactivate the elicitor-active oligogalacturonides, *Plant J.* (2018) 260–273, <https://doi.org/10.1111/tpj.13852>.
- [274] M. Frezzini, A. Scortica, M. Capone, D. Narzi, M. Benedetti, F. Angelucci, et al., Molecular dynamics simulations and kinetic measurements provide insights into the structural requirements of substrate size-dependent specificity of oligogalacturonide oxidase 1 (OGO1), *Plant Physiol. Biochem.* 194 (2023) 315–325, <https://doi.org/10.1016/j.plaphy.2022.11.021>.
- [275] S. Osorio, C. Castillejo, M.A. Quesada, N. Medina-Escobar, G.J. Brownsey, R. Suau, et al., Partial demethylation of oligogalacturonides by pectin methyl esterase 1 is required for eliciting defence responses in wild strawberry (*Fragaria vesca*), *Plant J.* 54 (2008) 43–55, <https://doi.org/10.1111/j.1365-3113X.2007.03398.x>.
- [276] T. Shinya, R. Ménard, I. Kozone, H. Matsuoka, N. Shibuya, S. Kauffmann, et al., Novel β -1,3-, 1,6-oligoglucan elicitor from *Alternaria alternata* 102 for defense responses in tobacco, *FEBS J.* 273 (2006) 2421–2431, <https://doi.org/10.1111/j.1742-4658.2006.05249.x>.
- [277] O. Klarzynski, B. Plesse, J. Joubert, J. Yvin, M. Kopp, B. Kloareg, et al., Linear β -1, 3 glucans are elicitors of defense responses in tobacco, *Plant Physiol.* 124 (3) (2000) 1027–1037, <https://doi.org/10.1104/pp.124.3.1027>.
- [278] R. Ménard, S. Alban, P. de Ruffray, F. Jamois, G. Franz, B. Fritig, et al., β -1,3 glucan sulfate, but not β -1,3 glucan, induces the salicylic acid signaling pathway in tobacco and Arabidopsis, *Plant Cell* 16 (2004) 3020–3032, <https://doi.org/10.1105/tpc.104.024968>.
- [279] A. Gauthier, S. Trouvelot, J. Kelloniemi, P. Frettinger, D. Wendehenne, X. Daire, et al., The sulfated laminarin triggers a stress transcriptome before priming the SA- and ROS-dependent defenses during grapevine's induced resistance against *Plasmopara viticola*, *PLoS One* 9 (2) (2014), <https://doi.org/10.1371/journal.pone.0088145>.
- [280] D.Z. Delgado, M.B. de Freitas, M.J. Stadnik, Effectiveness of saccharin and ulvan as resistance inducers against rust and angular leaf spot in bean plants (*Phaseolus vulgaris*), *Crop Prot* 47 (2013) 67–73, <https://doi.org/10.1016/j.cropro.2013.01.003>.
- [281] M.C. de Borba, M.B. de Freitas, M.J. Stadnik, Ulvan enhances seedling emergence and reduces *Fusarium* wilt severity in common bean (*Phaseolus vulgaris* L.), *Crop Prot* 118 (2019) 66–71, <https://doi.org/10.1016/j.cropro.2018.12.014>.
- [282] R.G. Chiquito-contreras, M. Murillo-amador, S. Carmona-hermandez, C.J. Chiquito-contreras, L.G. Hernandez-montiel, Effect of marine bacteria and ulvan on the activity of antioxidant defense enzymes and the bio-protection of papaya fruit against *Colletotrichum gloeosporioides*, *Antioxidant* 8 (580) (2019), <https://doi.org/10.3390/antiox8120580>.
- [283] R. Paulert, R. Ascrizzi, S. Malatesta, P. Berni, M.D. Nosedá, M.M. de Carvalho, et al., *Ulva intestinalis* extract acts as biostimulant and modulates metabolites and hormone balance in basil (*Ocimum basilicum* L.) and parsley (*Petroselinum crispum* L.), *Plants* 10 (1391) (2021), <https://doi.org/10.3390/plants10071391>.
- [284] A. Shomron, D. Duanis-Assaf, O. Galsurker, A. Golberg, N. Alkan, Extract from the macroalgae *Ulva rigida* induces table grapes resistance to *Botrytis cinerea*, *Foods* 11 (723) (2022), <https://doi.org/10.3390/foods11050723>.
- [285] S. Caillot, S. Rat, M.L. Tavernier, P. Michaud, J. Kovensky, A. Wadouachi, et al., Native and sulfated oligoglucuronans as elicitors of defence-related responses inducing protection against *Botrytis cinerea* of *Vitis vinifera*, *Carbohydr. Polym.* 87 (2) (2012) 1728–1736, <https://doi.org/10.1016/j.carbpol.2011.09.084>.
- [286] C. El Modafar, M. Elgadda, R. El Boutachfai, E. Abouraicha, N. Zehhar, E. Petit, et al., Induction of natural defence accompanied by salicylic acid-dependant systemic acquired resistance in tomato seedlings in response to bioelicitors isolated from green algae, *Sci. Hortic.* 138 (2012) 55–63, <https://doi.org/10.1016/j.scienta.2012.02.011>.
- [287] E. Abouraicha, Z. El Alaoui-Talibi, R. El Boutachfai, E. Petit, B. Courtois, J. Courtois, et al., Induction of natural defense and protection against *Penicillium expansum* and *Botrytis cinerea* in apple fruit in response to bioelicitors isolated from green algae, *Sci. Hortic.* 181 (2015) 121–128, <https://doi.org/10.1016/j.scienta.2014.11.002>.
- [288] V. Jaulneau, C. Laffite, C. Jacquet, S. Fournier, S. Salamagne, X. Briand, et al., Ulvan, a sulfated polysaccharide from green algae, activates plant immunity through the jasmonic acid signaling pathway, *J. Biomed. Biotechnol.* (2010), <https://doi.org/10.1155/2010/525291>.
- [289] E.A. Mousavi, F. Nasibi, K.M. Kalantari, Stimulation effect of carrageenan on enzymatic defense system of sweet basil against *Cuscuta campestris* infection, *J. Plant Interact.* 12 (1) (2017) 286–294, <https://doi.org/10.1080/17429145.2017.1341560>.
- [290] L. Mercier, C. Laffite, G. Borderies, X. Briand, M.T. Esquerré-Tugayé, J. Fournier, The algal polysaccharide carrageenans can act as an elicitor of plant defence, *New Phytol.* 149 (2001) 43–51, <https://doi.org/10.1046/j.1469-8137.2001.00011.x>.
- [291] J.S. Sangha, S. Ravichandran, K. Prithiviraj, A.T. Critchley, B. Prithiviraj, Sulfated macroalgal polysaccharides λ -carrageenan and ι -carrageenan differentially alter *Arabidopsis thaliana* resistance to *Sclerotinia sclerotiorum*, *Physiol. Mol. Plant Pathol.* 75 (2010) 38–45, <https://doi.org/10.1016/j.pmp.2010.08.003>.
- [292] J.S. Sangha, S. Kandassamy, W. Khan, N.S. Bahia, R.P. Singh, A.T. Critchley, et al., λ -Carrageenan suppresses tomato chlorotic dwarf viroid (TCVDv) replication and symptom expression in tomatoes, *Mar. Drugs* 13 (2015) 2875–2889, <https://doi.org/10.3390/md13052875>.
- [293] J. Vera, J. Castro, R.A. Contreras, A. González, A. Moenne, Oligo-carrageenans induce a long-term and broad-range protection against pathogens in tobacco plants (var. Xanthi), *Physiol. Mol. Plant Pathol.* 79 (2012) 31–39, <https://doi.org/10.1016/j.pmp.2012.03.005>.
- [294] J.S. Sangha, W. Khan, X. Ji, J. Zhang, A.A.S. Mills, A.T. Critchley, et al., Carrageenans, sulphated polysaccharides of red seaweeds, differentially affect *Arabidopsis thaliana* resistance to *Trichoplusia ni* (Cabbage looper), *PLoS One* 6 (10) (2011), <https://doi.org/10.1371/journal.pone.0026834>.
- [295] K.C. Li, X.Q. Zhang, Y. Yu, R.E. Xing, S. Liu, P.C. Li, Effect of chitin and chitosan hexamers on growth and photosynthetic characteristics of wheat seedlings, *Photosynthetica* 58 (3) (2020) 819–826, <https://doi.org/10.32615/ps.2020.021>.

- [296] S. Basa, M. Nampally, T. Honorato, S.N. Das, R. Podile, N. Eddine, et al., The pattern of acetylation defines the priming activity of chitosan tetramers, *J. Am. Chem. Soc.* (2020), <https://doi.org/10.1021/jacs.9b11466>.
- [297] G.T. Tziros, A. Samaras, G.S. Karaoglaniadis, Laminarin induces defense responses and efficiently controls olive leaf spot disease in olive, *Molecules* 26 (1043) (2021), <https://doi.org/10.3390/molecules26041043>.
- [298] T.C. Cairns, X. Zheng, P. Zheng, J. Sun, V. Meyer, Turning inside out: filamentous fungal secretion and its applications in biotechnology, agriculture, and the clinic, *J. Fungi* 7 (535) (2021), <https://doi.org/10.3390/jof7070535>.
- [299] K. Rantsiou, S. Giacosa, M. Pugliese, V. Englezos, I. Ferrocino, S. Río Segade, et al., Impact of chemical and alternative fungicides applied to grapevine cv Nebbiolo on microbial ecology and chemical-physical grape characteristics at harvest, *Front. Plant Sci.* 11 (700) (2020), <https://doi.org/10.3389/fpls.2020.00700>.
- [300] C. Pagliarani, A. Moine, W. Chitarra, G.R. Meloni, S. Abba, L. Nerva, et al., The molecular priming of defense responses is differently regulated in grapevine genotypes following elicitor application against powdery mildew, *Int. J. Mol. Sci.* 21 (6776) (2020), <https://doi.org/10.3390/ijms21186776>.
- [301] R. Balestrini, S. Ghignone, G. Quiroga, V. Fiorilli, I. Romano, G. Gambino, Long-term impact of chemical and alternative fungicides applied to grapevine cv Nebbiolo on berry transcriptome, *Int. J. Mol. Sci.* 21 (6067) (2020), <https://doi.org/10.3390/ijms21176067>.
- [302] J.-C. Cabrera, A. Boland, P. Cambier, P. Frettinger, P. van Cutsem, Chitosan oligosaccharides modulate the supramolecular conformation and the biological activity of oligogalacturonides in Arabidopsis, *Glycobiology* 20 (6) (2010) 775–786, <https://doi.org/10.1093/glycob/cwq034>.
- [303] G. van Aubel, R. Buonatesta, P. van Cutsem, COS-OGA: a novel oligosaccharidic elicitor that protects grapes and cucumbers against powdery mildew, *Crop Prot* 65 (2014) 129–137, <https://doi.org/10.1016/j.cropro.2014.07.015>.
- [304] A. Clinkemaillie, A. Decroës, G. van Aubel, S.C. dos Santos, M.E. Renard, P. van Cutsem, et al., The novel elicitor COS-OGA enhances potato resistance to late blight, *Plant Pathol.* 66 (2017) 818–825, <https://doi.org/10.1111/ppa.12641>.
- [305] S. Moreau, G. van Aubel, R. Janky, P. van Cutsem, Chloroplast electron chain, ROS production, and redox homeostasis are modulated by COS-OGA elicitation in tomato (*Solanum lycopersicum*) leaves, *Front. Plant Sci.* 11 (2020) 597589, <https://doi.org/10.3389/fpls.2020.597589>.
- [306] P. Melis, K. Stoffels, M. Vervoort, T. Van Delm, Integrated approach of powdery mildew control on strawberry cultivar ‘Elsanta’ in Belgium, *Acta Hort.* 1156 (104) (2017) 709–714, <https://doi.org/10.17660/ActaHortic.2017.1156.104>.
- [307] A.R. Bergamaschi, F. Cavazza, R. Bugiani, Optimization of copper applications using laminarine for the sustainable control of grape downy mildew, in: *BIO Web of Conferences*, vol. 50, EDP Sciences, 2022 03005, <https://doi.org/10.1051/bioconf/20225003005>.
- [308] O. Taibi, V. Bardelloni, F. Bove, F. Scaglia, T. Caffi, V. Rossi, Activity of resistance inducers against *Plasmopara viticola* in vineyard, in: *BIO Web of Conferences*, vol. 50, EDP Sciences, 2022 03003, <https://doi.org/10.1051/bioconf/20225003003>.
- [309] B.W.G. Stone, E.A. Weingarten, C.R. Jackson, The role of the phyllosphere microbiome in plant health and function, *Annu. plant rev. online* 1 (2) (2018) 533–556, <https://doi.org/10.1002/9781119312994.apr0614>.
- [310] L. Nerva, C. Pagliarani, M. Pugliese, M. Monchiero, S. Gonthier, M.L. Gullino, et al., Grapevine phyllosphere community analysis in response to elicitor application against powdery mildew, *Microorganisms* 7 (662) (2019), <https://doi.org/10.3390/microorganisms7120662>.
- [311] D.-E. Miliordos, M. Tsiknia, N. Kontoudakis, M. Dimopoulou, C. Bouyioukos, Y. Kotsieris, Impact of application of abscisic acid, benzothiadiazole and chitosan on berry quality characteristics and plant associated microbial communities of *Vitis vinifera* L var. Mouhrtaro plants, *Sustainability* 13 (5802) (2021), <https://doi.org/10.3390/su13115802>.

Standard Abbreviations

ABA: abscisic acid
 AM: arbuscular mycorrhizal
 BR: brassinosteroid
 CEBiP: chitin elicitor binding protein
 CERK: chitin elicitor receptor kinase
 DAMP: damage-associated molecular pattern
 DA: degree of acetylation
 DP: degree of polymerization
 ET: ethylene
 ETI: effector-triggered immunity
 GA: gibberellic acid
 LPS: lipopolysaccharide
 LRR: leucine-rich repeat receptor
 LysM: lysin motif
 JA: jasmonic acid
 MAPK: mitogen-activated protein kinase
 MLG: mixed linkage glucan
 NO: nitric oxide
 OGA: oligogalacturonide
 PA: pattern of acetylation
 PAMP: pathogen-associated molecular pattern
 PGN: peptidoglycan
 PRR: pattern recognition receptor
 PTI: pattern-triggered immunity
 RLCK: receptor-like cytoplasmic kinase
 RBOHD: respiratory burst oxidase protein D
 RLK: receptor-like kinase
 RLP: receptor-like protein
 ROS: reactive oxygen species
 SA: salicylic acid
 TF: transcription factor
 WAK: wall-associated kinase