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Review

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Plant Cell Wall-Derived Damage-Associated Molecular Patterns as Emerging Immune Elicitors for Sustainable Crop Protection

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Abstract: Synthetic pesticides have long contributed to global agricultural productivity over the past decades. However, the widespread reliance on chemical control strategies based on synthetic pesticides has raised serious concerns regarding pesticide resistance, non-target toxicity, environmental persistence, and the resulting decline in agricultural sustainability. In response, biopesticides have emerged as eco-friendly alternatives, among which biochemical pesticides acting as immune elicitors represent a promising new paradigm. Rather than exerting direct biocidal activity, these compounds activate plant innate immunity and thereby confer durable resistance with minimal ecological impact. Among immune elicitors, cell wall- and cuticle-derived damage-associated molecular patterns (hereafter, CW-DAMPs, as used in this review) are increasingly recognized as key endogenous signals linking structural integrity sensing to immune activation. Upon damage to the extracellular barrier, CW-DAMPs are released and recognized by cell-surface pattern recognition receptors (PRRs), which initiate downstream immune signaling involving Ca^{2+} influx, reactive oxygen species (ROS) production, and mitogen-activated protein kinase (MAPK) activation. Recent studies have begun to elucidate the molecular mechanisms underlying CW-DAMP generation and perception. However, the structural diversity and full spectrum of CW-DAMPs derived from complex extracellular polymers remain insufficiently characterized. This review integrates recent findings on the biogenesis, perception, and signaling of CW-DAMPs, highlights their potential applications, and discusses the current challenges and future perspectives for developing CW-DAMP-based biopesticides as sustainable tools for crop protection.

Keywords: Biochemical pesticides, Biopesticides, Cell wall–derived damage–associated molecular patterns, Immune elicitors, Innate immunity

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Introduction

Over the past several decades, improvements in global agricultural productivity have relied heavily on the use of synthetic pesticides, which provide rapid and cost-effective control of pests and diseases. However, the synthetic pesticide-based chemical control systems have generated multifaceted challenges, including the emergence of pesticide resistance in target pests and pathogens, toxicity to non-target organisms, environmental persistence, and increasingly stringent regulatory restrictions, ultimately undermining agricultural sustainability [1-4]. Accordingly, there is an increasing demand to shift toward low-risk, environmentally friendly pest and disease management strategies that can simultaneously support food production and environmental conservation [5]. In this context, biopesticides have emerged as major alternatives to synthetic pesticides, and among them, biochemical pesticides that do not directly kill pests and pathogens but instead activate plant innate immunity are being recognized as a key enabling technology for sustainable agriculture [6]. These immune elicitors promote plant's intrinsic immune responses by inducing reactive oxygen species (ROS) production, activating mitogen-activated protein kinase (MAPK) signaling pathways, and upregulating the expression of defense-related genes, thereby conferring broad-spectrum resistance against diverse pathogens [7].

In particular, damage-associated molecular patterns (DAMPs) derived from the plant extracellular barrier–including cell wall- and cuticle-derived fragments (hereafter collectively referred to as CW-DAMPs in this review)–represent a major class of endogenous danger signals released upon pathogen infection or physical perturbation of these protective layers. These molecules are perceived by plasma membrane-localized pattern recognition receptors (PRRs) and elicit pattern-triggered immunity (PTI)-like responses [8]. Reported or putative CW-DAMPs include pectin-derived oligogalacturonides (OGs) [9,10]; cellulose-derived cellodextrins [11]; and diverse hemicellulose-derived oligosaccharides, such as xylan-derived xylo-oligosaccharides (XOS), arabinoxylan-derived arabinoxylan-oligosaccharides (AXOS) [12], xyloglucan-derived xyloglucan oligosaccharides (XGOs) [13], and mannan/glucomannan-derived mannan-oligosaccharides (MOS) [14]. In addition, Poaceae-specific β-1,3/1,4-glucan-derived oligosaccharides have been reported [15]. Cuticle-derived cutin monomers and oligomers, originating from the cuticle as a functionally coupled outer layer of the cell wall, have also been proposed as important DAMPs [16]. Collectively, these molecules function as key mediators linking cell wall integrity sensing to immune activation [17,18], and they provide an important scientific foundation for the development of immunity-inducing biochemical pesticides based on endogenous signals [6].

In this review, we comprehensively summarize CW-DAMPs with respect to their origin-dependent classes, recognition mechanisms, downstream signaling pathways, and applications and commercialization examples, and we further discuss their potential utility within integrated pest management (IPM) frameworks as well as future research directions.

Limitations of Synthetic Pesticides

Synthetic pesticides have made substantial contributions to improving global agricultural productivity over the past several decades. These products are primarily composed of chemically synthesized compounds and are commonly classified–according to their targets–into insecticides, fungicides, and herbicides [19]. Because they can suppress pests and diseases rapidly and effectively, and can be manufactured at industrial scale, synthetic pesticides have been widely adopted in agricultural practice [20]. Following the introduction of organochlorine pesticides in the 1940s, subsequent development of organophosphates, carbamates, pyrethroids, and later neonicotinoids and phenylpyrazoles further diversified both the spectrum and modes of action of synthetic pesticides [21]. Meanwhile, substantial increases in crop yields have been reported in Europe and the United States alongside the adoption of pest and disease control technologies during the mid-to-late twentieth century [22], suggesting that synthetic pesticides contributed not merely as auxiliary inputs but as a major pillar supporting global food security [23].

However, the widespread use of synthetic pesticides has been accompanied by adverse consequences, including resistance development, harm to non-target organisms, environmental persistence, and risks to human health [1,2]. Repeated application of products with the same mode of action has accelerated the selection of resistance mechanisms in pest and pathogen populations –such as target–site alterations and enhanced metabolic detoxification–thereby creating a vicious cycle in which increasingly potent formulations are introduced in response to diminishing efficacy [24]. In addition, synthetic pesticides can exert broad toxicity toward non-target biota-including pollinators, natural enemies, and aquatic organisms–and their transport and accumulation in soil and aquatic environments can disrupt ecosystem structure and reduce biodiversity [2]. Furthermore, certain environmentally persistent compounds can accumulate along food chains through biomagnification [25], and long-term human exposure has been

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associated with neurological and endocrine dysfunction as well as carcinogenicity [26]. Collectively, these environmental and physiological risks expose the structural instability of agricultural systems that rely heavily on synthetic pesticides.

Awareness of these issues expanded globally following the publication of Rachel Carson's *Silent Spring* in 1962. Synthetic pesticides such as DDT (dichloro-diphenyl-trichloroethane) once contributed to the control of infectious diseases including malaria; however, concerns over ecosystem impacts driven by biomagnification and long-term persistence later intensified and catalyzed debates on environmental regulation [27]. Although *Silent Spring* centered more on public health and ecosystem toxicity than on plant disease control per se, this period marked the beginning of a broader reappraisal of 'dependence on synthetic pesticides' in crop protection. Since then, the international community has strengthened management of synthetic pesticide use while also pursuing the development of biological and nature-based control technologies; nevertheless, synthetic pesticide-based chemical control remains the dominant framework in global agriculture [3-5]. This persistence largely reflects the high cost-effectiveness of synthetic pesticides relative to alternative technologies [5] and their ability to deliver predictable control efficacy across diverse environments at relatively low cost [3]. Despite their short-term effectiveness, however, current synthetic pesticide–dependent crop protection systems continue to exhibit inherent vulnerabilities–such as resistance spread, non-target toxicity, and environmental persistence–that threaten long-term agricultural sustainability [28]. This recognition underpins calls for a paradigm shift from synthetic pesticide-based chemical control toward innate immunity-centered crop protection [28]. This shift has, in turn, fueled growing interest in biochemical pesticides, particularly immune elicitors.

Concept and Types of Biopesticides

Definition and advantages

Biopesticides refer to formulations that suppress pests and diseases by using active ingredients derived from biological sources, including microorganisms, plants, animals, and other naturally derived substances [29]. This term gained prominence in the late twentieth century, as environmental pollution and ecosystem disruption associated with the overuse of synthetic pesticides became increasingly recognized [5]. Early commercialization focused on microbial pesticides based on *Bacillus thuringiensis*, after which the scope expanded to include plant-based biopesticides, insect–pathogenic viruses, fungal metabolites, and related products [30]. More recently, the integration of biotechnological innovations–such as RNA interference (RNAi), nanoparticle–based formulations, and the utilization of endophytes–has driven rapid evolution of biopesticides from simple natural–product formulations toward integrated ecological approaches to crop protection that support sustainable agriculture [31-33].

In general, biopesticides are considered to pose lower risks to human health than synthetic pesticides and to exhibit reduced environmental persistence and biomagnification potential, with improved safety for non-target organisms [34,35]. Biopesticides are therefore widely regarded as environmentally benign agricultural inputs that align with the principles of green chemistry–namely, design guidelines aimed at reducing environmental burdens by minimizing the use and generation of hazardous substances, favoring renewable feedstocks, and improving biodegradability [35].

A related term, eco-friendly pesticides, encompasses pesticides designed to minimize environmental footprints and risks to human health regardless of whether their origin is chemical or biological [36]. Thus, while most biopesticides can be considered eco-friendly pesticides, eco-friendly pesticides are not necessarily biopesticides [37]. In this review, we define biopesticides as formulations that satisfy both environmental safety and a biological origin. We then discuss how this concept has recently been extended and refined in the context of immunity-inducing biochemical pesticides.

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Major Categories

Microbial pesticides

Microbial pesticides are formulations derived from microorganisms, including bacteria, fungi, viruses, and protists [28,38]. They control target pests and pathogens by disrupting their physiology and development or through infection and parasitism, and therefore are generally considered to pose relatively lower risks to applicators and public health. For example, *B. thuringiensis* produces δ-endotoxins that display insect larva-specific toxicity [39], whereas *Beauveria bassiana* and *Metarhizium anisopliae* penetrate the host cuticle, invade the internal body cavity, and ultimately induce host death through parasitism [40]. In addition, baculoviruses act primarily against lepidopteran larvae [41], and entomopathogenic nematodes of the genus *Steinernema* express pathogenicity by infecting hosts in association with symbiotic bacteria [42]. Nevertheless, microbial products are often sensitive to environmental conditions and may exhibit limited storage stability, leading to practical constraints in formulation development, distribution, and field application [39,43]. Despite these limitations, microbial pesticides are regarded as a core component of sustainable agricultural systems because of their ecological safety and target specificity.

Plant-based biopesticides

Plant-based biopesticides are formulations that control pests and pathogens using bioactive substances obtained from diverse plant tissues, including leaves, roots, seeds, and flowers [44]. These agents are typically essential oils or secondary metabolites (e.g., alkaloids, terpenes, and flavonoids) and act against pests and pathogens by deterring feeding, disrupting neurotransmission, or exhibiting antibacterial and antifungal activities [45]. Plant-based biopesticides are generally biodegradable and exhibit relatively low toxicity to non-target organisms, offering environmental advantages [46]. However, their efficacy can be difficult to standardize because it is sensitive to weather conditions, application concentration, and chemical variability in source materials [45]. For instance, pyrethrins–natural insecticidal compounds derived from *Chrysanthemum cinerariifolium*–block neural transmission in insects, resulting in selective toxicity [47]. Azadirachtin, extracted from neem (*Azadirachta indica*), suppresses feeding by acting on insect chemoreceptors and induces developmental abnormalities by disrupting signaling pathways of ecdysteroids and juvenile hormones [48]. In addition, a wide range of extracts from weeds and medicinal plants has been reported to inhibit pest reproduction or development, highlighting their potential value as next-generation resources for natural crop protection products [49,50].

Biochemical pesticides

Biochemical pesticides are defined as formulations that suppress the occurrence of pests and diseases using biologically derived active substances [51,52]. They achieve control either by non-toxically disrupting physiological processes in target pests and pathogens (e.g., development, behavior, and reproduction) or by activating the plant’s intrinsic immune responses. Rather than exerting direct biocidal activity, these products achieve control by selectively modulating targeted physiological functions [53-55] and are characterized by high target specificity and relatively low risks to non-target organisms [56]. Based on their modes of action, biochemical pesticides can be classified into semiochemicals (e.g., pheromones), hormone analogs or regulators, plant growth regulators, and enzymes or proteins. These compounds act through diverse physiological and behavioral routes, including mating disruption, developmental inhibition, suppression of feeding and digestion, and induction of repellency, and can also stimulate plant defense signaling to promote intrinsic immune responses [57]. Thus, biochemical pesticides are increasingly viewed not only as natural–product–based control agents but also as tools that activate or prime plant innate immunity to enhance resistance against diverse pests and pathogens. In particular, recent advances in our understanding of CW-DAMPs and the PRRs that perceive them have recast the mode of action of immunity-inducing biochemical pesticides, bringing renewed attention to these products through the lens of plant innate immunity activation [6].

Mode of action of immune-inducing biochemical pesticides

Plants lack circulating immune cells and adaptive immune components found in animals, yet they have evolved a sophisticated innate immune system that detects external cues at the cellular level and initiates innate immune responses [58]. The first layer of plant innate immunity is pattern-triggered immunity (PTI), which is activated when plasma membrane-localized PRRs perceive pathogen-associated molecular patterns (PAMPs) [8,59,60]. The second layer is effector-triggered immunity (ETI), which is induced when nucleotide-binding leucine-rich repeat proteins (NLRs) in the cytosol detect pathogen-secreted effectors [61-63].

PTI constitutes the most fundamental layer of plant defense, enabling rapid recognition of invading pathogens and initiation of intracellular defense signaling. Upon PTI activation, a complex and highly coordinated cascade of responses is triggered, including Ca^{2+} influx, ROS production, MAPK activation, transcription factor activation, and induction of defense-related gene expression. Together, these responses establish a basal defense barrier that broadly restricts pathogen establishment, proliferation, and tissue invasion [64-66]. By conferring resistance against diverse classes of pathogens, PTI provides broad-spectrum resistance and basal immunity [60,67].

Importantly, PTI can be induced not only by non-self PAMPs but also by endogenous DAMPs generated upon cellular damage [68]. DAMPs are molecules released when cellular structures are disrupted by pathogen infection and associated processes, including enzymatic degradation and physical perturbation. These signals are perceived by PRRs in neighboring cells, thereby activating PTI [18,67]. Representative DAMPs include extracellular ATP (eATP), protein fragments (e.g., high mobility group proteins), peptides (e.g., PAMP-induced peptide 1), and CW-DAMPs (cell wall- and cuticle-derived DAMPs) [69-71]. In particular, CW-DAMPs serve as key signals linking cell wall integrity sensing to immune activation and will be discussed in detail in later sections.

Meanwhile, PTI can be suppressed by pathogen-delivered effectors [61]. In such cases, plants detect these effectors directly or indirectly through cytosolic NLRs and activate ETI [60,72]. ETI represents a second defensive tier that counteracts pathogen strategies aimed at evading PTI [73]. Compared with PTI, ETI elicits stronger and more sustained defense responses [61,73,74] and is frequently accompanied by localized programmed cell death, manifested as the hypersensitive response, which effectively restricts pathogen spread [75]. Defense signaling activated during ETI can further expand into systemic acquired resistance (SAR), thereby enhancing immune competence throughout the plant [76,77].

Recent studies indicate that PTI and ETI do not operate as independent modules but instead form an interacting network that modulates the amplitude and duration of each response, functioning as an integrated immune platform [63,78,79]. This multilayered immune architecture, initiated by PTI and reinforced by ETI, provides a central framework for understanding the mode of action of plant immunity-inducing biochemical pesticides and establishes a scientific foundation for sustainable, immunity-based crop protection strategies.

Classes of CW-DAMPs by Origin

Biochemical pesticides that activate plant innate immunity can target diverse signaling pathways to strengthen the plant's innate immune system [11]. Among these, CW-DAMPs have attracted particular attention because they constitute endogenous signals that directly reflect damage to the plant's extracellular barriers-the cell wall and cuticle [80]. A key feature of CW-DAMPs is that they can activate defense responses via PRRs without relying on pathogen-derived cues; this property highlights CW-DAMPs as a molecular class of immune elicitors with especially clear structural and functional definitions. CW-DAMPs are generated when polysaccharides in the extracellular cell wall matrix–such as pectin, cellulose, and hemicelluloses–are cleaved by diverse cell wall-degrading enzymes, including polygalacturonases, pectate lyases, xylanases, xyloglucan endohydrolases, and mannanases. In parallel, damage to the cuticle can generate cutin-derived fragments (e.g., cutin monomers/oligomers) through enzymatic or physicochemical breakdown, which likewise function as DAMPs in activating immune responses. In the following sections we

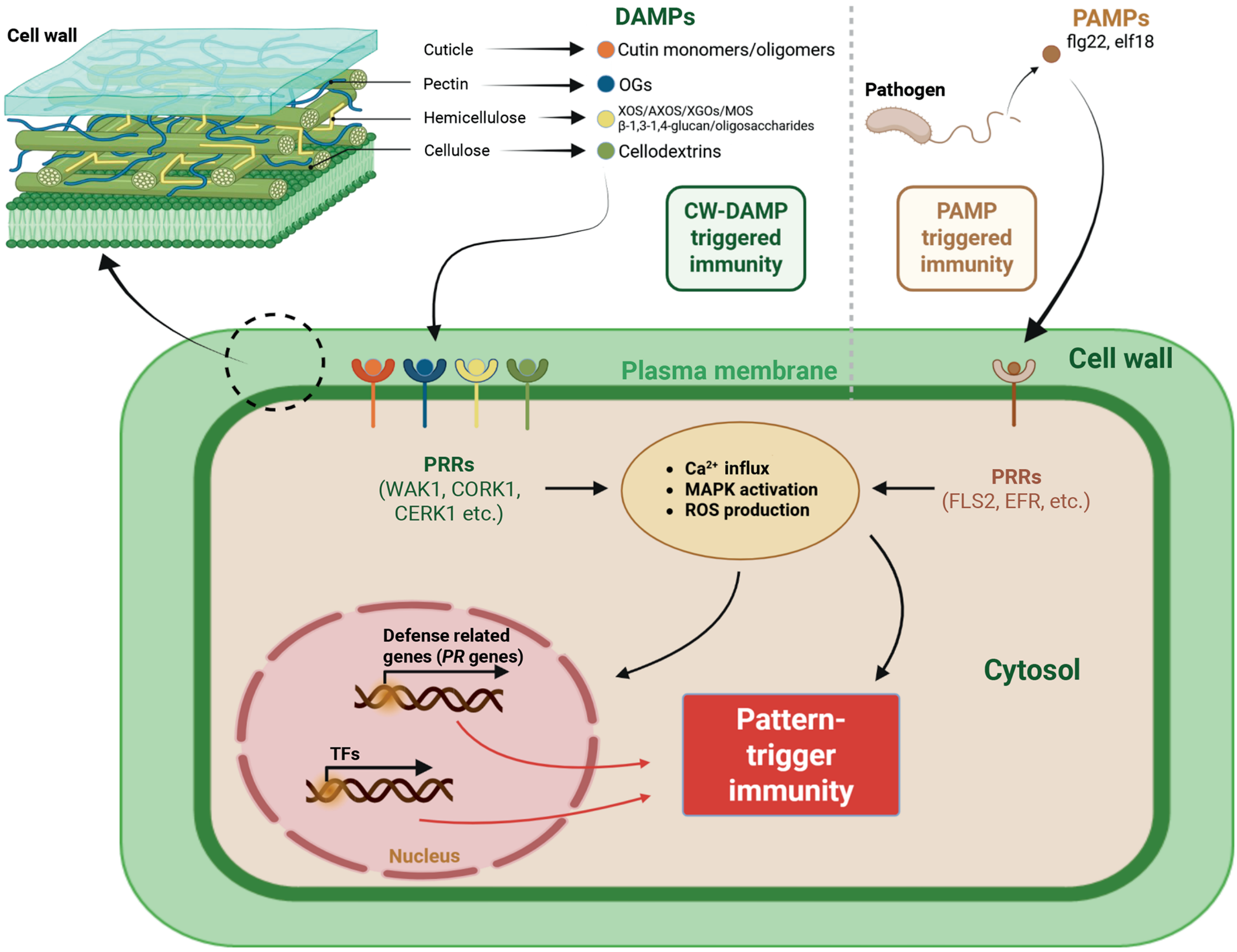

Fig. 1. Schematic representation of plant immune activation by cell wall- and cuticle-derived damage-associated molecular patterns (CW-DAMPs).

Upon pathogen infection or mechanical damage, structural polymers in the cell wall–such as pectin, cellulose, and hemicellulose–are depolymerized to release CW-DAMPs, including oligogalacturonides (OGs), cellodextrins, xylo-oligosaccharides (XOS), and other hemicellulose-derived fragments. In parallel, disruption of the cuticle results in the release of cutin-derived fatty acid monomers and oligomers. These CW-DAMPs are perceived by pattern recognition receptors (PRRs) on the plasma membrane–such as wall-associated kinase 1 (WAK1), cellooligomer receptor kinase 1 (CORK1), chitin elicitor receptor kinase 1 (CERK1)–which activate canonical early immune responses, including Ca^{2+} influx, reactive oxygen species (ROS) production, mitogen-activated protein kinase (MAPK) activation, and the transcription of defense-related genes. Through these coordinated signaling events, CW-DAMPs function as endogenous indicators of structural damage and activate pattern-triggered immunity (PTI), linking damage perception in both the cell wall and cuticle to innate immune activation.

summarize the major CW-DAMP classes reported to date and their biogenesis mechanisms, organized by the constituent components of the cell wall and cuticle.

Pectin-derived

The plant cell wall forms a composite polysaccharide network in which cellulose microfibrils provide a load-bearing scaffold that is embedded in and surrounded by a matrix primarily composed of pectins and hemicelluloses [81,82]. Among these components, pectin is a major structural matrix polysaccharide enriched in the primary cell wall and the middle lamella, where it plays key roles in cell-cell adhesion and in regulating wall porosity [83,84].

When cell wall-degrading enzymes secreted by pathogens, such as polygalacturonases or pectin lyases, cleave the homogalacturonan domain of pectin, oligogalacturonides (OGs) are released [9,10]. OGs are a representative class of CW-DAMPs generated upon cell wall damage, and they have been reported to be perceived by the plasma membrane-localized wall-associated kinase 1 (WAK1) [85,86]. Activation of WAK1 triggers downstream defense signaling, leading to canonical PTI-like responses, including Ca^{2+} influx, production of ROS and nitric oxide, phytoalexin accumulation, and induction of defense-related gene expression [87-89].

Recent work in *Arabidopsis thaliana* showed that OG-induced immune responses are not completely abolished in *wak1/2/3/4/5* quintuple mutants, suggesting that OG perception and/or signaling may involve additional WAK family members and/or co-receptors rather than relying exclusively on WAK1 [80]. Nevertheless, OG treatment has been consistently observed to elicit PTI-like responses and enhance disease resistance across multiple plant species.

The bioactivity of OGs depends strongly on their degree of polymerization (DP) and the methyl-esterification status of the parental pectin. In general, OGs of intermediate length (typically DP ~10-15) have been reported to induce the strongest immune responses [90,91]. Moreover, lower levels of pectin methyl-esterification facilitate cleavage by polygalacturonases, increasing OG production and consequently amplifying defense responses [85].

Cellulose-derived

Cellulose is a high-molecular-weight polysaccharide composed of β-1,4-linked D-glucose units that assemble into crystalline microfibrils [92]. As the central load-bearing framework of the layered cell wall architecture, these microfibrils confer wall strength and tensile resistance. These microfibrils interact with hemicelluloses and pectins to form a composite polysaccharide network that supports cell shape maintenance and contributes to protection against external stresses [93].

When cellulose microfibrils are cleaved during pathogen infection, mechanical perturbation, cellulose biosynthesis defects, or cellulase-mediated degradation, low-molecular-weight β-1,4-glucan oligosaccharides (cellodextrins) are released from the cell wall [11,94,95]. In *Arabidopsis*, these molecules are perceived by the plasma membrane-localized cellooligomer receptor kinase 1 (CORK1), which activates downstream defense signaling [11,96]. Following CORK1 activation, cells exhibit Ca^{2+} influx, ROS production, MAPK phosphorylation, and induction of transcription factors and defense-related genes, culminating in canonical PTI-like responses [11,96]. The optimal DP of cellodextrins varies among plant species; for example, cellotriose (DP 3) is reported to be most active in *Arabidopsis*, whereas oligomers with DP 6-7 show the highest activity in grapevine [96,97]. Such differences may reflect structural variation in receptor-ligand interactions [98].

Hemicellulose-derived

Hemicelluloses are major polysaccharides of the plant cell wall matrix and include xylans, xyloglucans, and mannans/glucomannans [99]. By forming hydrogen bonds with cellulose microfibrils, these polymers modulate the mechanical strength and flexibility of the cell wall and contribute to the structural stability of the wall network. During pathogen infection or enzymatic degradation, hemicellulose chains can be cleaved by various cell wall-degrading enzymes, including xylanases, xyloglucanases, and mannanases, thereby releasing diverse hemicellulose-derived oligosaccharide fragments. Some of these fragments are thought to function as CW-DAMPs [13].

The best-studied hemicellulose-derived CW-DAMPs are xylan-derived xylo-oligosaccharides (XOS). XOS elicit canonical PTI-like responses-including ROS production, MAPK phosphorylation, callose deposition, and induction of defense-related genes-n multiple plant species, including *Arabidopsis*, rice (*Oryza sativa*), and *Brachypodium distachyon* [100]. Notably, a recent study showing that xylanase-generated XOS broadly induce such responses supports the view that XOS can act as a widely conserved CW-DAMP across plant species [12,97]. Arabinoxylan-derived arabinoxylan-oligosaccharides (AXOS) have likewise been reported to function as CW-DAMPs. AXOS trigger Ca^{2+} influx, ROS production, MAPK activation, and defense gene induction, and enhance disease resistance in tomato (*Solanum lycopersicum*) and pepper (*Capsicum annuum*), with 3^3-α-L-arabinofuranosyl-xylotetraose (XA_3XX) exhibiting the highest activity [12]. Together, XOS and AXOS-closely related in both structure and function-indicate that xylan/arabinoxylan-based matrices are not merely structural materials but also important sources of immune-activating signals.

Xyloglucan-derived xyloglucan oligosaccharides (XGOs) have also been reported to function as CW-DAMPs. XGOs generated by degradation of the xyloglucan backbone by xyloglucan endohydrolase (XEH) induce PTI-like responses, including ROS production, MAPK activation, callose deposition, and defense gene induction, and enhance disease resistance in grapevine (*Vitis vinifera*) and *Arabidopsis* [13]. These findings support the classification of XGOs as CW-DAMPs and underscore that the xyloglucan matrix is an important source of immune-activating signals rather than merely a structural accessory. Moreover, XGOs have been implicated in the concurrent regulation of growth- and defense-associated signaling, suggesting a role in mediating the growth-defense trade-off [13,101]. For example, treatment of tobacco (*Nicotiana tabacum*) cells with XGOs induces the expression of jasmonate ZIM-domain protein 8 (JAZ8), a transcriptional repressor of jasmonate responses, together with defense-associated chitinase-like genes [101], indicating that xyloglucan fragments may couple immune activation to cellular growth regulatory pathways.

Mannan-oligosaccharides (MOS), generated by cleavage of mannan/glucomannan, have also been identified recently as a new class of CW-DAMPs. MOS induce canonical PTI-associated outputs–including Ca^{2+} influx, ROS production, activation of MAPK signaling, induction of defense-related gene expression, and enhanced disease resistance in rice and tobacco–and are considered functionally analogous to other hemicellulose-derived immune-activating signals such as XOS, AXOS, and XGOs [14].

In grasses (Poaceae), lineage-enriched wall polymers include mixed-linkage β-1,3/1,4-glucan and arabinoxylan-based heteroxylans. Among these, mixed-linkage β-1,3/1,4-glucan–often treated as a Poaceae-enriched hemicellulosic component distinct from classical hemicelluloses–can be degraded during pathogen infection to generate β-glucan oligosaccharides [15]. These β-glucan oligosaccharides have been reported to be perceived by OsCERK1. This perception promotes formation of the OsCERK1-OsCEBiP receptor complex with chitin elicitor-binding protein (OsCEBiP) and triggers PTI outputs such as ROS production, MAPK activation, defense gene induction, and enhanced disease resistance in rice.

Cuticle-derived

The plant cuticle, an outer extracellular layer composed of cutin and waxes, forms a composite lipidic barrier that overlays the cell wall, and serves as a primary physical barrier limiting pathogen ingress and water loss [102]. Cutin is a high-molecular-weight polyester mainly built from C_{16}-C_{18} hydroxy- and epoxy-fatty acids that are cross-linked via ester bonds into a three-dimensional network [103,104].

When the cutin polymer is cleaved by pathogen-secreted cutinases or by physical perturbation, cutin-derived fatty-acid monomers and oligomers are released [103,105]. These lipid-based fragments have been reported to act as extracellular, non-carbohydrate DAMPs, inducing early immune responses in cells surrounding damaged sites, including Ca^{2+} influx, ROS production, MAPK activation, and induction of defense-related gene expression [16]. For example, cutin hydrolysates isolated from multiple plant species–including cucumber (*Cucumis sativus*), tomato, and apple (*Malus domestica*)–have been shown to trigger ROS production, with dodecan-1-ol derived from cucumber cutin exhibiting the highest activity [106]. These observations suggest that cutin breakdown products released by cutinase activity during pathogen infection can function as immune elicitors.

In addition, expression of a fungal cutinase in the cell wall of *Arabidopsis* has been reported to confer strong resistance to the fungal pathogen *Botrytis cinerea* [107]. This resistance was described as operating independently of major defense hormone pathways mediated by salicylic acid, ethylene, and jasmonic acid, and was accompanied by secretion of antifungal compounds and enhanced expression of genes encoding defense-related proteins such as lipid transfer proteins, peroxidases, and protein inhibitors [107]. Taken together, cuticle-derived cutin monomers/oligomers represent a prominent class of extracellular, non-carbohydrate DAMPs that contribute to the rapid activation of early immune responses upon barrier damage. These findings further support the view that the cuticle, together with the cell wall, constitutes a key immune surveillance interface for sensing structural damage at the plant cell surface.

CW-DAMP Recognition Receptors and Signaling

Although different CW-DAMPs are perceived by distinct PRRs, their downstream defense responses substantially overlap with canonical PTI signaling, including Ca^{2+} influx, ROS production, and MAPK activation [60,68]. Accordingly, this section provides an integrated overview of PRRs implicated in CW-DAMP recognition and the associated signaling pathways.

The concept of DAMPs originated from the observation that certain endogenous molecules elicit PTI-like defense responses through 'pattern recognition'. Consistent with this framework, receptors that perceive DAMPs are likewise considered members of the PRR category [60,65,67,108]. Thus, although PAMPs and DAMPs differ in origin, they can be viewed as two classes of ligands that converge on a shared pattern-recognition-based signaling architecture. This perspective suggests that plant PTI has expanded beyond sensing pathogen-derived cues (PAMPs) to include recognition of self-derived damage signals (DAMPs), and is increasingly viewed as an integrated immune recognition system that encompasses both ligand classes [67,80,96,109-111].

PRRs are broadly classified-based on structural features–into receptor-like kinases (RLKs) and receptor-like proteins (RLPs) [112]. RLKs possess an intracellular kinase domain that directly transduces recognition events via phosphorylation and typically comprise an N-terminal signal peptide, a single transmembrane region, and a C-terminal cytoplasmic kinase domain [113,114]. In contrast, RLPs lack an intracellular kinase domain and often transmit signals through interaction with adapter kinases [115,116]. Both classes carry extracellular recognition domains, with representative examples including leucine-rich repeats (LRRs), malectin-like domains, lysin motifs (LysMs), and epidermal growth factor (EGF)-like repeats [117]. *Arabidopsis* CORK1 is an LRR-malectin-type RLK bearing a composite extracellular domain composed of malectin-like and LRR modules [96], as well as a single transmembrane region and a cytoplasmic kinase domain. OsCERK1 is a LysM-type RLK characterized by an extracellular domain containing three LysM motifs, a single transmembrane region, and an active kinase domain [15]. *Arabidopsis* WAK1 is an EGF-type RLK with an extracellular region containing EGF-like repeats and a pectin-binding GUB/WAK-binding domain, together with a single transmembrane region and a cytoplasmic kinase domain [80].

In multiple plant species, including *Arabidopsis*, tomato, and rice, PAMP perception commonly involves recruitment of co-receptors such as brassinosteroid insensitive 1-associated kinase 1 (BAK1/SERK3), which form complexes with PRRs and amplify

Table 1. Overview of major CW–DAMP types, their origins, processing enzymes, PRRs, signaling outputs, and immune responses

CW–DAMP Type	Origin	PRR	Signaling	Immune Responses	References
Oligogalacturonides	Pectin	WAK1	Ca^{2+}, ROS/NO	Defense gene expression Phytoalexin accumulation	[87], [88], [89]
Cellodextrins	Cellulose	CORK1	Ca^{2+}, ROS, MAPK	TF induction Defense gene expression	[11], [96]
Xylo-oligosaccharides	Hemicellulose/Xylan	Unknown	ROS, MAPK	Callose deposition Defense gene expression	[100]
Arabinoxylan-oligosaccharides	Hemicellulose/Arabinoxylan	Unknown	Ca^{2+}, ROS, MAPK	Defense gene expression Enhanced disease resistance	[12]
Xyloglucan oligosaccharides	Hemicellulose/Xyloglucan	Unknown	ROS, MAPK	Callose deposition TF induction Defense gene expression Enhanced disease resistance	[13], [101]
Mannan oligosaccharides	Hemicellulose/Mannan	Unknown	Ca^{2+}, ROS, MAPK	Defense gene expression Enhanced disease resistance	[14]
β-1,3-1,4-glucan-derived oligosaccharides	Hemicellulose/Poaceae-specific β-1,3-1,4-glucan	CERK1–CEBiP	ROS, MAPK	Defense gene expression Enhanced disease resistance	[15]
Cutin monomers/oligomers	Cuticle	Unknown	Ca^{2+}, ROS, MAPK	Defense gene expression Enhanced disease resistance	[16], [106], [107]

Note: cell wall- and cuticle-derived damage-associated molecular pattern (CW-DAMP), pattern recognition receptor (PRR), reactive oxygen species (ROS), nitric oxide (NO), mitogen-activated protein kinase (MAPK), transcription factor (TF) signaling through reciprocal phosphorylation [118,119]. However, for CW-DAMP perception, co-receptor dependency has not yet been clearly defined. For example, *Arabidopsis* CORK1, which mediates cellodextrin perception, has been reported not to interact directly with BAK1 [11], and the OsCERK1-OsCEBiP complex, which perceives β-glucan oligosaccharides derived from mixed-linkage β-1,3/1,4-glucan, also mediates BAK1-independent signaling [15]. These cases suggest that CW-DAMP pathways may employ distinct co-receptor configurations or even co-receptor-independent signaling modes compared with canonical PAMP-PRR systems [96].

Translational Perspective: From the Laboratory to the Field

Field deployment and commercial examples

Research on CW-DAMP-based immune elicitors has recently moved beyond laboratory-scale basic studies toward industrial application, with commercial formulations being deployed across diverse crops [120]. These products are classified as low-risk biopesticides that can replace or complement conventional synthetic pesticides, owing to their low chemical toxicity and a relatively low likelihood of selecting for resistance development in pathogens [121]. In particular, CW-DAMP formulations are positioned as biochemical pesticides of plant origin that activate the plant's innate immune system, and they are increasingly recognized as key components of environmentally friendly integrated pest management (IPM) programs [122].

Representative commercialized examples include Planticine® and FytoSave®. Planticine® uses pectin-derived OGs as the primary active ingredient, and it has been reported to enhance both fungal resistance and fruit quality in tomato [123]. FytoSave® is a commercial product based on a chitosan-OG complex; its efficacy against powdery mildew in grapevine and cucumber has been validated, and it has shown stable control performance even when co-applied with copper- and sulfur-based pesticides [124,125]. Collectively, these cases illustrate the ongoing translation of CW-DAMP-based immune elicitors from laboratory research to agricultural practice.

Patent and regulatory trends

CW-DAMP-based immune-elicitor technologies are rapidly diffusing beyond basic research, with commercialization and patenting accelerating their development. In particular, low-molecular-weight oligosaccharides derived from cell wall polysaccharides such as pectin and cellulose are being leveraged as representative CW-DAMPs, and efforts to improve field deployability increasingly focus on controlling the degree of polymerization, enabling enzymatic production, and enhancing formulation stability.

For example, CN101481717A (2009) proposed a strategy in which pectin-derived OGs are applied to *Artemisia annua* cell cultures to promote biosynthesis of artemisinin, an antimalarial compound. This represents an early applied case indicating that CW-DAMPs can stimulate endogenous signaling networks to modulate secondary metabolic pathways. Subsequently, US20230270110A1 (2023) reported the use of oxidative cellulose oligosaccharides (e.g., cellobionic acid) generated by lytic polysaccharide monooxygenases (LPMOs) as plant immune elicitors. US20240065266A1 (2024) further described an enzymatic approach to produce OGs with a DP 2-10, proposing a strategy to simultaneously promote crop growth and enhance disease resistance. In addition, EP3780957B1 (2023) covers a composite formulation combining CW-DAMPs with SAR-inducing factors, and it has been positioned as a next-generation immune enhancer that integrates PTI and SAR.

In parallel, policy and regulatory frameworks are being established rapidly. The European Union's Regulation (EC) No 1107/2009 defines procedures for approval of active substances and market entry for plant protection products (PPPs) and includes a 'low-risk active substances' category that institutionally supports commercialization of naturally derived and bio-based materials. The U.S. Environmental Protection Agency (EPA) likewise operates a biopesticide registration framework that separately classifies and regulates natural substances, biochemical pesticides, and microbial pesticides, thereby reducing burdens associated with development and registration. Together, these international regulatory systems provide policy-level support for the commercialization potential of CW-DAMP-based immune elicitors. Overall, CW-DAMP technologies are establishing an industrial ecosystem centered on patenting, productization, and institutionalization, suggesting that CW-DAMPs are evolving into a core platform for next-generation, immunity-inducing biopesticides aimed at sustainable agriculture.

Nevertheless, several structural limitations remain. First, efficacy can be variable: the performance of CW-DAMP-based immune elicitors differs depending on crop species, pathogen type, and environmental conditions, making it challenging to achieve consistent control outcomes [126]. Second, the intrinsic instability of CW-DAMPs has been highlighted as a major constraint for field deployment, and formulation development therefore often requires protective and/or encapsulation technologies to mitigate degradation and improve durability [127]. Third, field performance can be particularly inconsistent: while stable effects are commonly observed under controlled conditions such as greenhouses, efficacy in open-field conditions has been reported to fluctuate substantially due to interacting factors including climate, soil conditions, disease pressure, and resident microbial communities [124]. These observations suggest that CW-DAMP-mediated immune activation is finely modulated by physiological and environmental variables, and addressing this complexity remains a key challenge for future practical implementation.

Conclusions and Future Perspectives

CW-DAMPs serve as a mechanistic link between cell wall damage sensing and immune signaling, and they are becoming established as key endogenous signals that bridge plant immunity research with technologies for sustainable agriculture [120]. Recent studies have rapidly elucidated CW-DAMPs, their cognate PRRs, and downstream signaling pathways at genetic and biochemical levels, and have shown that these pathways substantially overlap with canonical PTI signaling [6,96,128]. These advances suggest that CW-DAMPs are not merely “damage indicators” but function as major regulatory signals that shape plant defense responses.

CW-DAMP-based immune elicitors are attracting attention as eco-friendly immunity-inducing strategies with the potential to replace conventional chemical pesticides, owing to their low toxicity, reduced propensity to drive resistance development, and ability to induce broad-spectrum disease resistance [121]. In particular, within IPM frameworks, CW-DAMP-based formulations are expected to provide synergy when combined with preventive cultural practices, resistant cultivars, and biological control, while enabling complementary use of minimal amounts of chemical pesticides when necessary to improve control stability and cost-effectiveness. Nevertheless, technical constraints-including environmental dependence of efficacy, instability of the active materials, and variability arising during formulation-remain major barriers to commercialization [124,126,127].

To overcome these limitations, foundational research must be further expanded, including discovery of new CW-DAMP candidates across diverse cell wall polysaccharides and cuticle components, elucidation of structure-activity relationships, integrated analysis of PRR-mediated signaling networks, and quantitative modeling of the magnitude and durability of immune responses. In parallel, advancing process and formulation technologies to improve field deployability-such as precise control of optimal DP, stabilization and controlled-release formulations, and nanoparticle-based delivery matrices-will be critical determinants of practical implementation. Building on these advances, developing composite immune strategies that combine CW-DAMPs with existing synthetic elicitors and/or resistance-breeding approaches is also emerging as an important direction. Moreover, for CW-DAMP-based products to be used reliably as biopesticides/immune elicitors within IPM programs, internationally harmonized standards for efficacy validation, safety assessment, and regulatory alignment will need to be established and adopted.

In summary, CW-DAMP research is transitioning from a ‘discovery phase’ to a ‘precision regulation phase’. As new CW-DAMPs are identified and integrated with technologies that fine-tune immune signaling, CW-DAMP-based immune elicitors are poised to reduce reliance on synthetic pesticides and to become core components of sustainable crop protection strategies within IPM frameworks.

Data Availability: All data are available in the main text or in the Supplementary Information.

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