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Posted Date: 23 November 2023

doi: 10.20944/preprints202311.1458.v1

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Review

Plant-Derived Antimicrobial Peptides: A Plant Defense Weapon against Biotic and Abiotic Stresses

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Abstract: Global agriculture has been forced to increase food production to feed the growing human population, while confronting various environmental obstacles such as global warming, resistance to pathogens, and constraints on arable land caused by soil salinity, drought, rising sea level, saltwater intrusion, and urbanization. Regarding abiotic stresses, salinity is a worldwide problem for agricultural production. Many efforts, therefore, have been made to cope with the environmental challenges, however, the progress of salinization, which is mainly caused and accelerated by anthropogenic activities, is likely faster than our progress in finding ways to deal with this problem. In addition, drought represents a global threat to the production of major crops. In addition, pests and pathogens cause significant crop losses and diminish global food security. Among the various strategies that have been investigated and applied in plant science, antimicrobial peptides derived from plants have caught widespread attention from scientists since these peptides exhibit beneficial biological activities. In agricultural science, there have been reports on the roles of antimicrobial peptides with active properties against biotic and abiotic stresses. Non-specific plant lipid transfer proteins, thionins, systemins, defensins, cyclotides, and heveins-like antimicrobial peptides are common antimicrobial peptides that have been found to be involved in the defense system against fungi and insect pests. Based on their potential ability to protect crops from pests, bacteria, and pathogenic fungi, the use of antimicrobial peptide genes in creating transgenic plants has been largely conducted during the last decades, and these studies have obtained positive results against the growth of fungi and bacteria. This review will focus on the latest progress in studies of antimicrobial peptides related to biotic and abiotic stress tolerance in plants. We will also update the current progress in the development of antimicrobial peptide-based transgenic crops.

Keywords: plant-derived antimicrobial peptides; biotic and abiotic stresses; salinity; drought; pathogenic fungi; plant diseases; insect pests; transgenic plants

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1. Introduction

The world's agricultural system needs to dramatically increase its productivity to satisfy the nutrient demands of an estimated 8.5 x 10^9 inhabitants in 2025 [1]. Furthermore, the increase in *per capita* income in various developing countries has intensified the requirement for food supply in terms of both quantity and quality [2]. In contrast, the global agricultural production is suffering from various environmental challenges such as pest pressure [3], soil pollution [4], ground water pollution

[5], shortage of fresh water for irrigation [6], drought [7], and salinity stress [8]. Among these ecological threats, salinity has largely been considered as one of the crucial burdens on agriculture worldwide as it dramatically diminishes the productivity of crop plants or even destroys crop production [9]. Currently, the area of global land affected by salinity, to some extent, exceeds 8.31-11.73 million km^2 [10]. Drought stress, which is caused by global warming and reduced precipitation, is becoming one of the main limiting factors of plant growth and yield [11]. In addition, the loss of global crop production caused by phytopathogens, and pests is 20–40%, which accounts for $290 billion per year [12]. The injudicious application of synthetic chemical pesticides and antibiotics poses a threat to human health, environmental pollution, and the development of pesticide resistance [13–15]. Furthermore, chemical agents adversely affect the population of beneficial soil microbes such as *Enterobacter*, *Aeromonas*, *Comamonas*, *Stenotrophomonas*, *Bordetella*, and *Staphylococcus* [16]. These severe circumstances urge agricultural scientists to find nonconventional sources for protecting important crops. The diversity, ubiquity, and versatility of plant-derived antimicrobial peptides (PAMPs) make them abundant pools for novel metabolite supply; these pools have potential applications in medicine, agriculture, and food industry [17–19]. Currently, a variety of strategies have been deployed to mitigate the adverse effects of biotic and abiotic stresses on plants. These strategies include plant breeding [20], acclimation[21], seed biopriming [22,23], plant growth-promoting rhizobacteria (PGPR) [24], and the application of non-protein amino acids (NPAAs) (e.g., 5-hydroxynorvaline, meta-tyrosine, GABA (c-aminobutyric acid), BABA (b-aminobutyric acid, Canavanine, L-DOPA, Mimosine, etc.) [25]. In addition to these approaches, research has focused on the effects of PAMPs on plant defense systems to improve resistance to phytopathogens [26], and on enhancing the adaptive mechanism to abiotic stresses [27] have been conducted. These studies have shown that PAMPs directly act as insecticidal molecules that inhibit the growth of insect larvae [28] or as inhibitors that suppress the growth of bacteria or pathogenic fungi [29]. Although the roles of PAMPs in the suppression of bacteria and fungi have been extensively investigated [30–32] their roles in reducing the negative effects of abiotic stresses appear to be neglected. In fact, not many papers have been found to work on the functions of PAMPs in improving plant tolerance to salinity and drought stress [33,34], heavy metals [35], and wound stress[36]. Transgenic crops have been developed over the past decades to integrate beneficial genes from bacteria, fungi, and other plant species into the host plant genomes. In addition to the well-known *Bt* genes from *Bacillus thuringiensis*, the PAMPs genes have also been widely used to provide new agronomic characteristics, including resistance to biotic and abiotic stresses [37]. In this review, we update the latest progress in the development of transgenic plants using PAMPs-encoding genes from different plant species to improve the resistance of important plants to biotic and abiotic stresses.

2. Thionins

2.1. Roles of thionins in mitigating biotic and abiotic stress

There are six major PAMP families, such as thionins, defensins, non-specific lipid transfer proteins, hevein, and knottin-like peptides, hairpinins and cyclotides. These families were classified based on the cysteine spacing motifs and 3-dimensional (3D) structures [38]. The family of thionins was the first PAMP whose antipathogenic properties were determined *in vitro*. These antimicrobial peptides are found only in some plant families of angiosperms and are composed of 6 or 8 cysteine residues (~5 kDa). The 3D folding pattern of thionins is stabilized by 6 to 8 disulfide-linked cysteines [38].

There are two action modes of thionins on pathogen cells: (i) Thionins interact with negatively charged phospholipids, such as phosphatidic acid or phosphatidyl serine, in the cell membrane [39]. The formation of a proteolipid complex induces membrane solubilization and lysis. Additionally, the withdrawal of phospholipids also interrupts the fluidity of the cell membrane, leading to irreparable lysis of the membrane [40]. (ii) Thionins insert into the membrane and act as a water channel through the αHTH double α-helix core. Water is allowed to pass through this narrow channel to the center of the bilayer membrane. However, it is then expelled from the center because of the random motion of phospholipids caused by repulsive interactions. This process frequently repeats, causing local membrane disintegration [41].

Decades ago, it was reported that a *Thi2.1* cDNA from *Arabidopsis thaliana*, expressed in the BVE-E6E7 bovine endothelial cell line, inhibited the viability (> 97%) of *Escherichia coli*, *Staphylococcus aureus*, and *Candida albicans* [42]. A thionin-like peptide from *Capsicum annuum*, called CaThi, had a strong suppressive effect against *Candida* spp. with half-maximal inhibitory concentrations (IC_{50}) of 10 to 40 µg/mL [43]. CaThi was also found to permeabilize the plasma membrane in all tested *Candida* species and to induce oxidative stress in *C. tropicalis*. The synergistic effect between CaThi and fluconazole significantly enhanced their candidacidal activity [43]. A 15 kDa-Thi2.4 protein from *A. thaliana* was found to interact with the virulence factor, fungal fruit body lectin (FFBL), of *Fusarium graminearum*, thereby reducing the toxicity of *F. graminearum*, in addition to the known antifungal property of Thi2.4 [44]. In the bird cherry oat aphid-resistant barley Hsp5 genotype, the transcript abundance of the thionin genes *THIO1567* and *THIO1570* was significantly greater than in the susceptible genotype Lina. Furthermore, the expression of *THIO1570* and *proteinase inhibitor (PI)* genes in the resistant breeding line BC1 exceeded that in the susceptible breeding line BC2. These genes were found to be constitutively expressed in the resistant genotypes, contributing to the resistance trait against the aphid (*Rhopalosiphum padi* L.) [45]. Upon nematode infection, thionin genes were suppressed earlier and more strongly than in the susceptible genotype (*Oryza sativa*) Nipponbare than in the resistant (*Oryza glaberrima*) accession TOG5681 [46]. Under drought stress conditions, the susceptible barley cultivar Concerto showed increased expression of the *HvTHIO1* gene [47]. A combination of osmotic and heat stress caused higher susceptibility of *Arabidopsis* plants to *Botrytis cinerea*, possibly due to the reduced expression of defense genes, including *PLANT DEFENSIN 1.3 (PDF1.3)*, *BOTRYTIS SUSCEPTIBLE 1 (BOS1)*, *THIONIN2.2 (THI2.2)*, and cell wall-related genes [48]. Thio-60 protein extracted from transgenic onion (*Allium cepa* L.) showed a higher inhibitory effect on spore germination of the fungus *Aspergillus niger*, with an inhibition of 52% compared to 37% of the non-transgenic protein [49]. Thionins also play roles in plant defense by perceiving pathogens and initiating signal transduction pathways. These pathways interconnect with a variety of defense processes that are regulated by phytohormones, such as salicylic acid (SA), jasmonic acid (JA), and ethylene [50].

2.2. Transgenic plants with thionin genes for enhanced biotic and abiotic stress tolerance

Thionin gene *Thi2.1*, encoding 5 kDa cysteine-rich antimicrobial peptides, was upregulated in the resistant Arabidopsis ecotype UK-4 upon *Fusarium oxysporum* f. sp. *matthiolae* infection, and its overexpression in susceptible Col-2 seedlings delayed chlorophyll loss, inhibited fungal growth, and caused severe abnormalities of the fungal phenotype [51]. The thionin gene *Thi2.1* was introduced into the tomato genome, generating transgenic plants with enhanced resistance to both Fusarium wilt (FW) (*F. oxysporum* f. sp. *lycopersici*) and bacterial wilt (BW) (*Ralstonia solanacearum*) [52]. In BW inoculation assay, the *RB7/Thi2.1* transgenic lines exhibited disease incidence comparable to the BW resistant variety H7996. Similarly, in FW inoculation test, *RB7/Thi2.1* transgenic lines R7 and R11 showed a disease severity similar to the FW resistant variety MH1 and significantly lower disease incidence than WT plants (Chan et al. 2005). β-purothionin, a member of thionins from wheat endosperm, is a 45-amino-acid residue peptide with 4 disulfide bonds and a high cationic charge, making it stable in environmental conditions. Transgenic Arabidopsis plants expressing the β-purothionin gene driven by a leaf-specific chloroplast carbonic anhydrase promoter displayed the highest resistance to *Pseudomonas syringae* strain DC3000 without any leaf infection symptoms. *In vitro* bioassays with *F. oxysporum* revealed that transgenic seedlings survived for 12–15 days with less necrosis and discoloration after fungal inoculation, compared to control seedlings which died within 6–8 days [53].

A barley α-hordothionin (*α-HT*) gene with 384 bp in length, driven by a strong constitutive promoter *El2Ω* or β-amylase (*β-Amy*) promoter (the 5'-UTR region), was transformed into the sweet potato cultivar Kokei No. 14, to confer the resistance trait to *Ceratocystis fimbriata* (Muramoto et al. 2012), the most damaging postharvest disease of sweet potato (*Ipomoea batatas* (L.) Lam.) [54]. To examine the resistance of the storage roots of the transgenic sweet potato to *C. fimbriata*, wounds were made and inoculated with a suspension of *C. fimbriata* spores. The black lesions of the transgenic *El2Ω: α-HT* No. 1 (119 mm^2) and *β-Amy: α-HT* No. 060201 (111 mm^2) were much smaller than those of the non-transgenic Kokei No. 14 (283 mm^2), indicating that the transgenic sweet potato lines acquired a new resistance trait to *C. fimbriata* [55]. Huanglongbing (HLB) is the most dangerous disease affecting global citrus production; thus, many efforts, including engineering plants with improved disease resistance, have been conducted extensively [56,57]. An endogenous citrus thionin gene was genetically modified to obtain *Mthionin* and transformed it into the Carrizo citrus genome to create transgenic Carrizo plants resistant to HLB disease and the citrus canker disease caused by *Candidatus* Liberibacter asiaticus (Las) and *Xanthomonas citri*, respectively [58]. Leaf infiltration assays showed that the *Mthionin* transgenic leaves displayed reduced or no canker development at low to high concentration of *X. citri* (10^4–10^7 CFU/mL). Compared to control plants, grafted plants with the transgenic Carrizo rootstock showed significantly lower Las titer young leaves and roots, indicating that *Mthionin* is a promising tool for HLB control [58]. In another study, the modified thionin (*Mthionin*) gene, driven by a double *35S* promoter, was inserted into the *A. thaliana* genome using the floral dip method [59]. The transgenic lines A24 and A52 had the highest Mthionin expression levels and showed reduced water soaking, lesions, and fungal biomass in detached leaf assays. After being sprayed with *F. graminearum* (5×10^5 conidia/mL), *GUS* transgenic plants developed severe symptoms (dry flowers, dry siliques, and dead branches), while *Mthionin* transgenic plants remained asymptomatic. Furthermore, *F. graminearum* conidia failed to germinate normally on *Mthionin* Arabidopsis leaves. At 48 h after inoculation, the expression of *DEFENSIN1.2* in *Mthionin* plants was significantly higher than in *GUS* plants, suggesting that *Mthionin* enhanced resistance to *Fusarium* spp. by regulating the defense genes and phytohormone signaling. Ectopic expression of two thionin genes *AK252675.1* and *AK359149* from barley in *Nicotiana benthamiana* reduced host susceptibility to *Myzus persicae*, which indicated the important role of thionin genes in resistance to aphids [60]. Recently, a *Thio-60* gene from *A. thaliana* was transformed into three date palm (*Phoenix dactylifera* L.) cultivars (Barhy, Sakkoti, and Shamia), resulting in transgenic date palm with higher resistance to *F. oxysporum*, as shown by pathogenicity test with *F. oxysporum* suspension on detached leaves [61].

To date, most studies have focused on the role of thionins in biotic stress resistance. Only a few papers have investigated the role of thionins in mitigating the toxicity of heavy metals to plants. Liu et al. (2023) showed that the defensin-dissimilar thionin gene *OsThi9* in rice was strongly expressed in roots, basal and middle stems, and growing seeds after exposure to 0.1 μM $CdCl_2$ for up to 7 days [62]. Overexpression of *OsThi9* in rice reduced the translocation of Cd from roots to shoots, thereby reducing Cd concentrations in the leaves, stems, and brown rice of the *OsThi9*-overexpressing plants grown in Cd-contaminated soil.

3. Defensins

3.1. Antimicrobial activities of defensins and their roles in enhancing abiotic stress tolerance in plants

Defensins, a well-studied family of PAMPs found in Brassicaceae, Fabaceae, and Solanaceae families, are small amphipathic cationic peptides with 45 to 54 amino acids (aa) and 8 conserved cysteine residues that form 4 disulfide bridges [63]. These disulfide bonds contribute to their stability under protease attack, a wide range of pH, and extreme temperatures [64]. Plant-derived defensins are classified as cis-defensin superfamily, while mammalian defensins belong to trans-defensin superfamily [65]. Defensin genes are differentially expressed during growth and development, in biotic and abiotic stress conditions, and in harmony with phytohormones [66]. The transcription factor *WRKY75* positively regulated the expression of defense-related genes in the JA signaling pathway, including *OCTADECANOID-RESPONSIVE ARABIDOPSIS (ORA59)* and *PLANT DEFENSIN* gene *PDF1.2*, as evidenced by the downregulation of these genes in *wrky75* mutants and their upregulation in *WRKY75*-overexpressing plants [67].

Like thionins, defensins use two antimicrobial strategies: membrane disruption and inhibition of cellular machinery. The γ-core motif is essential for the antimicrobial properties of defensins, as thoroughly reviewed by Slezina and colleagues [68,69]. In plants, the expression of defensins is triggered by the mitogen-activated protein kinase (MAPK) cascade, which is activated by two main responses: effector-triggered immunity (ETI) and MAMP-triggered immunity (MTI), in response to fungal and bacterial infection [70]. The defensin gene *CADEF1* was not expressed in healthy pepper leaves, but was induced by abiotic elicitors, such as H_2O_2, artificial wounding, salinity, and drought, stress hormones SA, methyl jasmonate (MeJA), JA, abscisic acid (ABA), and ET [70], and inoculation with virulent *Xanthomonas campestris* pv. *vesicatoria* [71]. The defensin genes *OsDEF7* and *OsDEF8* were highly upregulated by *Xanthomonas oryzae* pv. *oryzae* infection, and by abiotic stresses such as imbibition, anoxia, drought, cold, and dehydration [72]. In Arabidopsis leaves inoculated with *Alternaria brassicicola* or *P. syringae*, the expression of some defensin-like (DEFL) genes was highly upregulated, likely stimulated via JA signaling [73].

Protein Cp-thionin II, a plant defensin isolated from cowpea (*Vigna unguiculata*) seeds, exhibited bactericidal activity against *S. aureus* ATTC25923 (MIC of 128 μg/mL), *E. coli* ATTC 25922 (MIC of 64 μg/mL), and *P. syringae* (MIC of 42 μg/mL) [74]. DefSm2-D (KLCEKPSKTWFGNCGNPRHCGDQCKWEGVHGACHVRNGKHMCFCYFNCPQAE) is an antifungal protein from wild thistle (*Silybum marianum*) with a defensin domain [75]. To determine the antifungal activities of peptide fragments, truncated versions of DefSm2-D, such as SmAPα1-21 (KLCEKPSKTWFGNCGNPRHCG), SmAPα10-21 (WFGNCGNPRHCG), SmA-Pγ29-35 (GAVHGAC), and SmAPγ27-44 (WEGAVHGACHVRNGKHMC), were designed to determine the antifungal activities of peptide fragments. Among the truncated versions of DefSm2-D, SmAPγ27-44 exhibited the strongest antagonistic activity against *F. graminearum* with a MIC_{50} value of 20 μM, followed by SmAPα1-21 and SmAPα10-21 with MIC_{50} values of 32 μM and 70 μM, respectively. It was found that the Arg38 residue in the γ-core domain was dramatically important to the antifungal activity of defensin, which explained the highest antifungal effect of SmAPγ27-44 [76]. Additionally, the presence of 3 extra cationic Lysine (Lys) residues, 1 anionic Glutamic acid (Glu) residue, and one Tryptophan (Trp) residue in the SmAPα1-21 structure may account for its membrane interface capability. The site-specific binding targets on pathogen cell wall or cell membrane are critical for the further inhibition process of SmAPα1-21. Moreover, due to the difference in composition between fungal cell walls and host cells, SmAPα1-21 performs its selective activity only on the fungus, not on the host.

The scots pine (*Pinus sylvestris* L.) gene *PsDef5.1* was expressed in mature and immature seeds, in the seedling and reproductive organs such as male cones and pollen. The recombinant PsDef5.1 protein fused with a thioredoxin (Trx) had a cysteine rich α-motif (CX5CX3CX7CX9CXC) and a γ-core motif (GXCX9C), and expressed inhibitory activity against *F. sporotrichiella*, *B. cinerea*, *Phytophthora gonapodyides*, *Bacillus pumilus*, *Pectobacterium carotovorum* and *P. fluorescens* [66]. Plant defensins have been rarely studied in abiotic responses such as heavy metal exposure, but they have been shown to play a role in zinc tolerance, iron homeostasis, and disease resistance. In the shoots of the zinc-tolerant plant *Arabidopsis halleri* ssp. *halleri*, defensin proteins accumulated at high concentrations and defensin gene expression increased in response to Zn treatment [77]. The defensin gene *AtPDF1.1* was also upregulated in response to infection with the necrotropic bacterium *P. carotovorum* subsp. *carotovorum* (Pcc) [78]. *AtPDF1.1* was also involved in iron homeostasis because its expression was highly upregulated by iron overloading[78]. It was found that AtPDF1.1 endowed plant tolerance to Pcc by disturbing iron homeostasis via iron chelation [78]. Consequently, iron deficiency activated the iron-deficiency-induced ethylene signaling pathway, resulting in enhanced tolerance to Pcc. In contrast to the susceptible variety JG62, six defensin and defensin-like genes *CaDEF1.1B*, *CaDEF2.4*, *CaDEF2.5a*, *CaDEF3*, *CaDEF5*, and *CaDEFL2* were expressed at elevated levels in the resistant wild chickpea ICC17160 upon *F. oxysporum* f. sp. *ciceris* and *Rhizoctonia bataticola* infection [79]. These findings strongly suggest that these defensin genes play a role in both biotic and abiotic stress responses.

3.2. Transgenic plants with defensin genes for enhanced biotic and abiotic stress tolerance

doi:10.20944/preprints202311.1458.v1

The first attempt to transform defensin genes into plant genomes to increase resistance towards phytopathogenic fungi was made by Bondt et al. (1998) [80]. Since then, many defensins transgenic plants have been continuously generated by several research groups [81–86]. Recently, overexpression of the defensin gene *NaD1* from *Nicotiana alata* in tobacco (*Nicotiana tabacum*) var. Xanthi tobacco enhanced drought stress tolerance by maintaining photo-synthetic pigments and increasing antioxidant enzyme activity [87]. Under drought conditions, the *NaD1* transgenic tobacco lines showed a significant increase in the chlorophyll a, b contents, as well as the total chlorophyll content. In addition, the activities of the antioxidant enzymes catalase (CAT), peroxidase, ascorbate peroxidase (APX), and superoxide dismutase (SOD) in the transgenic lines were higher than in the non-transgenic line under drought stress. This resulted in a lower oxidative damage caused by elevated ROS accumulation.

Chelation is one of the main mechanisms for cadmium (Cd) detoxification in plants [88]. The defensin gene *AhPDF1.1* from the zinc hyperaccumulating plant *A. halleri* ssp. *halleri* was transformed into the *A. thaliana* under the control of the *35S* promoter, resulting in transgenic *A. thaliana* plants with increased Zn tolerance [77]. It was found that defensins *AtPDF2.6* in Arabidopsis and defensin *CAL2* in rice had Cd binding activity [88,89]. However, overexpression of *CAL2* in Arabidopsis conferred a Cd-sensitive phenotype. Similarly, overexpression of *CAL2* in rice did not enhance rice tolerance to Cd (Luo et al. 2020). In contrast, overexpression of AtPDF2.6 resulted in enhanced Cd tolerance in the transgenic Arabidopsis plants, while *Atpdf2.6* knockout mutants expressed higher sensitivity to Cd than the wild type (WT). The results suggest that AtPDF2.6 detoxifies cytoplasmic Cd through Cd chelation [88]. All eight cysteine residues in AtPDF2.5 were required for Cd tolerance and chelation, and the disruption of *AtPDF2.5* reduced Cd tolerance in plants [88]. Physiological analysis indicated that AtPDF2.5 promoted Cd efflux from the cytoplasm and regulated Cd accumulation in the cell wall [88].

4. Cyclotides

4.1. Antimicrobial activities of cyclotides and their roles in alleviating abiotic stress

Cyclotides are a series of plant-derived macrocyclic peptides, each with 28–37 aa and an embedded cystine knot. So far, cyclotides are found in five major plant families: Rubiaceae, Violaceae, Solanaceae, Cucurbitaceae, and Fabaceae [90]. Some cyclotide-like genes were also found in plants of the Poaceae family, i.e., *O. sativa*, *Zea mays*, *Triticum aestivum*, *Agrostis stolonifera*, *Schedonorus arundinaceus*, *Pennisetum glaucum*, *Sorghum bicolor*, *Hordeum vulgare*, *Saccharum offificinarum*, and *Setaria italica*. Cyclotides displayed high binding affinity to metals, and showed antiviral, antibacterial, and insecticidal properties [91]. The unique structure of cyclotides, e.g., a head-to-tail cyclic peptide backbone together with a cystine knot in which two disulfide bonds are linked by a third disulfide bond, allow them to dissolve in both organic and aqueous solvents, and to withstand extreme temperature, pH, and enzymatic degradation [92].

The cyclotide kalata B1 was isolated from 6 different plants, including *Oldenlandia affinis*, *Viola tricolor*, *Viola yedoensis*, *Viola philippica*, *Viola baoshanensis*, and *Viola odorata* and it was the first cyclotide reported and structurally characterized [92,93]. Historically, in some tribes in Congo, *O. affinis* was used as a medicinal tea to accelerate childbirth and was named after the name of the native medicine "kalata-kalata" in the Tsjiluba language [94]. Due to its remarkable stability, kalata B1 can resist boiling and harsh chemical and enzymatic conditions in the human digestive system. Cyclotides kalata B1 and kalata B2 from *O. affinis* were found to have insecticidal activity against *Helicoverpa punctigera* and *Helicoverpa armigera*, respectively [95,96]. Kalata B1 severely retarded the growth of *H. armigera* larvae at a low concentration (0.13% w/v) and caused a remarkable reduction in nutrient intake at a higher concentration (0.24% w/v). The ingestion of kalata B1 also caused severe changes in the midgut of *H. armigera* larvae, including the rupture of epithelial cells [97]. The changes in morphology of the midgut epithelial cells affected by kalata B1 resemble those induced by the δ-endotoxins from *B. thuringiensis* (*Bt*), a commonly used endotoxin to control insect pests [98]. Golden apple snail (*Pomacea canaliculata*), a dangerous herbivore of rice and native aquatic plants, is controlled using mechanical, agricultural, and chemical methods, including metaldehyde. However, metaldehyde is toxic to nontarget species, such as mammals [99]. Kalata B2, the most abundant cyclotide in *O. affinis* leaves, is more effective at killing golden apple snails than metaldehyde (LC_{50} of 53 µM vs. 133 µM) [100]. Cyclotides from the butterfly pea plant (*Clitoria ternatea*) can be used as eco-friendly insecticides. For example, the cyclotide Cter M, isolated from *C. ternatea* leaves and flowers, exhibited insecticidal activity against the cotton budworm *H. armigera*. In 2017, Sero-X®, a commercial bioinsecticide made from *C. ternatea* extracts, was approved for large-scale use in Australia [101]. Cycloviolacin (CyO2), a cyclopeptide produced by sweet violet (*Viola odorata* L.), has antagonistic activity against a variety of fungi and bacteria, including *Colletotrichum utrechtense*, *Alternaria alternata*, *F. oxysporum*, *Fusarium graminearum*, *Fusarium culmorum*, *Mycosphaerella fragariae*, *B. cinerea*, *P. syringae* pv. *syringae*, *Dickeya dadantii*, and *Pseudomonas atrosepticum*, with MICs varying from 0.8 to 100 µM. CyO2 uses two modes of action to control fungal and bacterial growth: membrane disruption and intracellular target interference [101].

Cyclotides are promising plant proteins with the potential to improve abiotic stress tolerance. However, their role in abiotic stress responses is still poorly understood and needs further investigation. *V. baoshanensis*, a plant species of the genus Viola, is a Cd hyperaccumulator [102]. The average Cd levels accumulated in the shoots and roots of this plant grown on lead-zinc mine were 1168 and 981 mg/kg biomass, respectively [103]. In *V. baoshanensis* leaves, the mRNA of the cyclotide precursor *VbCP7S* and its spliced version *VbCP6S* showed Cd-dependent upregulation patterns [104]. Similarly, the cyclotide-like genes *Zmcyc1* and *Zmcyc5* were induced by pathogenic fungi (e.g., *F. graminearum*, and *Ustilago maydis*), aphid infection (*Rhopalosiphum maydis*), abiotic stress (e.g., drought, salinity, and mechanical wounding), and phytohormones (e.g., SA and MeJA) in the maize leaves and stems [105]. The upregulation of cyclotide-like genes in maize after MeJA and SA treatment suggests that they are likely involved in plant defense systems like cyclotide genes.

4.2. The use of cyclotide genes in transgenic plant development to alleviate biotic and abiotic stresses

Five cyclotide precursor genes (*VbCP1-VbCP5*), together with a cysteine-rich small protein gene *Vb40* from *V. baoshanensis*, conferred copper (Cu) tolerance in the transgenic *Saccharomyces cerevisiae* YL36 [106]. This finding suggests that metal-binding proteins protect plants from heavy metal toxicity, thus endowing a higher metal tolerance to their hosts. The heavy metal binding capacity and metal tolerance of *Chlamydomonas reinhardtii* could be improved by transforming it with a class-II metallothionein (MT-II) from chicken[107]. As a result, the transgenic *C. reinhardtii* sequestered more Cd from the growth medium than the WT (9% vs. 5.5%) [107]. The kalata B1 (*Oak1*) gene from *Oldenlandia affinis* was transformed into seed-derived rice calli to produce transgenic rice plants that express the molluscicidal cyclotide kalata B1, which is toxic to the golden apple snail (*Pomacea canaliculata*) [108].

5. Hevein-like antimicrobial peptides

5.1. Antimicrobial activities and their roles in regulating abiotic stress response

Hevein-like antimicrobial peptides are a family of peptides that shares structural similarity with hevein, an AMP from the latex of rubber tree (*Hevea brasiliensis*) [109]. These peptides constitute a group of structurally related cysteine- and glycine-rich peptides in different plant families, including both monocots and dicots[110]. Hevein-like antimicrobial peptides have a chitin-binding domain that is involved in the binding to chitin and related oligosaccharides. The 40-aa Pn-AMP2 exhibited its antifungal proper-ties against chitin-containing and nonchitin-containing fungi [111]. A hevein-like protein PMAPI isolated from paper mulberry (*Broussonetia papyrifera*) displayed antifungal activity against *Trichoderma viride* with IC50 of 0.1 µg/µL [112]. Hevein-like plant peptides WAMP1 and WAMP2 in wheat (*T. kiharae* Dorof. et Migush) seeds were speculated to be involved in a defense response to biotic stress because they expressed antifungal activity, and their transcriptional patterns were highly upregulated in response to *F. oxysporum* infection [113]. The expression of the *wamp* genes was greatly induced by elevated NaCl levels (100–200 mM), suggesting the involvement of these

WAMP peptides in the salinity stress response[114]. Plants protect themselves against the negative effects of fungal proteases by producing WAMPs, which inhibit fungalysin, a secreted Zn-metalloproteinase from *F. verticillioides* that cuts plant IV chitinases at the chitin-binding site and catalytic domains, thereby degrading plant defense proteins [115]. The WAMP2-derived peptides from the central (WAMP-G1, WAMP-G2), N- (WAMP-N) and C-terminals (WAMP-C) of the WAMP2 structure intensified the activity of commercial fungicide Folicur® EC 250 (25% tebuconazole) against five fungi including *Fusarium culmorum*, *F. oxysporum*, *Bipolaris sorokininana*, *A. alternata*, and *Cladosporium cucumerinum* [116]. In addition, the combination of WAMP2-derived peptides, specifically WAMP-C, and Folicur® EC 250 had a synergistic effect on the suppression of spore germination, dramatically inhibiting the germination of the fungal spores (≥ 90%) [116]. Ginkgotide gB5, an 8C-hevein-like peptide from *Ginkgo biloba* leaves, showed an ability to hinder the growth of *A. niger*, *Curvularia lunata*, *Rhizoctonia solani*, and *F. oxysporum* with the IC_{50} values of 6.8, 10, 20, and 69.2 µg/mL, respectively [117].

5.2. The use of hevein-like antimicrobial peptide genes in transgenic plant development

To confer an improved resistance to *P. parasitica*, cDNA of pnAMP-h2 (583 bp) from *Pharbitis nil* (L.) Choisy seeds was transformed into the tobacco genome [118]. WjAMP1 protein purified from wasabi (*Wasabia japonica* L.) leaves demonstrated suppressive activities against fungi and bacteria [119]. The expression of *WjAMP1* was induced by fungal challenge with *A. alternata*, *B. cinerea*, and MeJA. Furthermore, the recombinant WjAMP1 was successfully expressed in *N. benthamiana* using the potato virus X vector. It inhibited the growth of various fungi in a dose-dependent fashion, including *A. alternata* (IC_{50} = 5.8 µg/mL), *B. cinerea* (IC_{50} = 15 µg/mL), *F. solani* (IC_{50} = 8.4 µg/mL), *Magnaporte grisea* (IC_{50} = 80 µg/mL). It also suppressed the growth of bacteria such as *E. coli* (IC_{50} = 27.5 µg/mL), *P. cichorii* (IC_{50} = 13.8 µg/mL), *P. glumae* (IC_{50} = 20 µg/mL), *P. plantarii* (IC_{50} = 22.5 µg/mL), and *A. tumefaciens* (IC_{50} = 12.5 µg/mL). A hevein-like AMP WAMP-1a from *T. kiharae* Dorof. et Migusch seed was expressed in *E. coli*. It exhibited antifungal activity against chitin-containing and chitin-free fungi (*F. solani*, *F. oxysporum*, *Bipolaris sorokiniana*) and antibacterial properties against Gram-negative (e.g., *P. syringae*, *Erwinia carotovora*) and Gram-positive bacteria (*Clavibacter michiganense*), and oomycete *Phytophthora infestans* [120]. Two genes encoding hevein-like antimicrobial peptides *amp1* and *amp2* were transformed into the tomato genome to obtain *P. infestans*-resistant plants[121]. The binary vector pB-AMP2 carrying a full length of *SmAMP2* from the chickweed (*Stellaria media*) was used for genetic transformation of tomato. Consequently, the lesion area in the *AMP2* transgenic tomato plants was much smaller than that in the non-transgenic plants (0.1 cm^2 vs. 0.96 cm^2). Stem wilt caused by *Phoma asponaqi* Sacc brings about severe disease on asparagus (*Asparagus officinalis* L.), resulting in dramatic economic losses. The hevein-like gene driven by the *35S* promoter was introduced into the asparagus genome using *A. tumefaciens* EHA105 [122]. The disease index of the transgenic asparagus plants was 42 ± 2.35% while that of non-transgenic plants was 75 ± 2.78%, suggesting that the hevein-like gene conferred an enhanced resistance to stem wilt. In addition, in the transgenic asparagus, the activities of antioxidant enzymes such as SOD, CAT, and phenylalanine ammonia lyase (PAL) were positively correlated with disease resistance, while the level of malondialdehyde was negatively correlated with the disease resistance. The 56-kDa MLX56 protein from the latex of mulberry plants has an extensin domain that is flanked by two hevein domains in its N region and C region[123]. *MLX56* transgenic tomato plants expressed antagonistic activity against *Spodoptera litura* larvae, western flower thrips *Frankliniera occidentalis*, and hadda beetle (*Henosepilachna vigintioctopunctata*), which suggest that the *MLX56* gene could be used as an anti-herbivory toxin in transgenic crops, along with the traditional *Bt* gene.

doi:10.20944/preprints202311.1458.v1

6. Systemins

6.1. Roles of systemins in plant immunity

Systemin (SYS) is an 18-aa hormone that is processed from a 200-aa prosystemin (PS) [124]. In tomato plants, the SYS went through a long distance (40 cm) from the injection site to the top at a spread speed of 2.5 cm/h [125]. SYS from tomato triggered resistance to the necrotrophic fungus *Plectosphaerella cucumerina* via JA-signaling pathway [126]. When infected with *P. cucumerina*, the activity of JA-biosynthesis gene *LOX2* was significantly induced by SYS. BAK1 and BIK1 are membrane receptors that can be used as PAMP-triggered immunity markers [127]. In the normal condition, neither BAK1 nor BIK1 was regulated by SYS. Upon *P. cucumerina* treatment, however, the SYS-treated plants demonstrated elevated expression levels of BAK1 and BIK1. Likewise, an increased production of H_2O_2 was observed in the SYS-treated plants after the treatment of flagellin 22 (flg22). This suggests that SYS is perceived by Arabidopsis in a novel mode of perception, unlike classical damage-associated molecular patterns. In the 10-day-old Arabidopsis seedlings treated with 5 μM SYS, the JA-responsive gene *JASMONATE ZIM-DOMAIN PROTEIN 10 (JAZ10)*, the pathogen-responsive gene *DEFENSIN1.2 (PDF1.2)*, and *DEFENSIN1.3 (PDF1.3)* were notably induced relative to those in untreated control [128]. Additionally, Zhang et al. (2018) noticed that the expression of *PDF1.2* occurred concurrently with the activation of the JA-signaling pathway and with an enhanced resistance to *B. cinerea* [128]. Furthermore, the overexpression of the tomato *prosystemin (PS)* gene in Arabidopsis conferred higher resistance to *B. cinerea* than that in WT plants, suggesting that the PS gene acted as a modulator of JA-responsive genes to activate plant immune response to necrotrophic fungi [128]. The exogenous supply of SYS peptide to tomato plants via foliar spraying or root uptake through hydroponic culture constrained the growth and development of *Spodoptera littoralis* larvae over several generations [129]. The application of non-self SYS also reduced leaf colonization caused by *B. cinerea* and attracted more natural enemies by a blend of volatile compounds [129]. More recently, the exogenous application of PS peptide to tomato plants has been shown to increase the mortality of *S. littoralis* and reduce the colonization of *B. cinerea* [130]. These findings indicate that PS, in addition to SYS, can protect plants from the attack of insects and fungi.

Hydroxyproline-rich systemins (HypSys) are small defense signaling glycopeptides that were first isolated in the Solanaceae family [131]. HypSys isolated from tobacco (*N. tabacum*) and tomato (*Solanum lycopersicum*) were found to induce defense genes against herbivore attack [132]. These defense-signaling glycopeptides were also found in petunia (*Petunia hybrida*) leaves, where they were named PhHypSys. Although PhHypSys did not induce antiherbivore protease and polyphenol oxidase activities like tobacco and tomato HypSys peptides, they instead triggered the elevated regulation of *defensin I* gene, which is involved in inducible defense responses against pathogens [133].

6.2. The use of systemin genes in transgenic plant development

PS, previously regarded as simply a precursor to SYS, has recently been discovered to contain biologically active regions. A truncated PS (*tPS*) cDNA, with the SYS sequence deleted, was transformed into tomato genome to confer resistance to insects and pathogenic fungi [130]. As a result, *S. littoralis* larvae that fed on *tPS* transgenic tomato leaf disks had impaired growth and higher mortality rates than the control group [130]. The *tPS* transgenic tomato plants also showed the suppressive effect on *B. cinerea* growth, thereby reducing necrosis areas on leaves [130]. Moreover, microarray and RT-qPCR showed that the *tPS* tomato had high expression levels of cell wall-related genes, as well as cytoskeletal element genes. Previously, a *tPS* cDNA from tomato was successfully transformed into tobacco cv. Samsun to confer an enhanced resistance to *B. cinerea* [134]. RT-qPCR revealed that, at 6 h after mechanical wounding, genes encoding heat shock protein (HSP), glutathione S-transferase (GST), and proteinase inhibitor (PI) II, were highly upregulated in the *tPS* tomato compared to the non-transgenic tomato[134]. The roles of HSP, GST, and PIs in plant protection have been widely established [135–137]. For example, proteinase inhibitors have largely been used to protect plants from the attack of insects [138]. GSTs play roles in detoxification of toxic substances, transport of auxins, and attenuation of oxidative stress [139]. Under biotic stress, HSP helps to accumulate and stabilize pathogenesis-related (PR) proteins [140].

7. Plant non-specific lipid transfer proteins

7.1. Antimicrobial activities and their roles in regulating abiotic stress response

Plant non-specific lipid transfer proteins (nsLTPs) play crucial roles in plant growth, development, and biotic and abiotic stress responses. nsLTPs are a member of the PR-14 family. They are small proteins (6.5–10.5 kDa) with a hydrophobic nature and a conserved motif of eight cysteines. The eight-cysteine motif is shown as C-Xn-C-Xn-CC-CXC-Xn-C-Xn-C, where "X" represents any amino acid and "n" indicates the number of amino acid residues. These amino acids are linked by four disulfide bonds to form conserved alpha helices in nsLTPs. The structure of nsLTPs renders stability, enhances capability to bind to, and transports diverse hydrophobic molecules. C-terminal calmodulin (CaM) and calmodulin-like proteins (CMLs) are ubiquitous Ca^{2+} sensors that bind to Ca^{2+} ions to regulate cellular processes and molecules involved in plant stress responses, in response to fluctuations in intracellular Ca^{2+} concentration, which are cell signals for plants to react appropriately to environmental stimuli [141]. nsLTPs contain a calmodulin (CaM)-binding domain and phosphorylation sites. When CaM binds to the CaM-binding domain on nsLTPs, it triggers a signal transduction cascade that regulates important processes in plants [142]. The transcription of the wheat genes *TaLTPIb.1*, *TaLTPIb.5*, and *TaLTPId.1* was regulated by a variety of stress hormones, including salicylic acid (SA), methyl jasmonate (MeJA), indole-3-acetic acid (IAA), and ABA. *TaLTPIb.1* and *TaLTPIb.5* were induced by wound, drought, cold stress, and SA, but repressed by MeJA, IAA, and ABA, respectively. *TaLTPId.1* was triggered by dark treatment, SA, and MeJA, but depressed by IAA [143]. The SiLTP gene from foxtail millet (*Setaria italica*) is involved in plant responses to salt and drought stress via an ABA-dependent pathway. SiLTP transcription is highly upregulated by ABA, polyethylene glycol, and NaCl. Electrophoretic mobility shift assays, and yeast one-hybrids showed that the transcription factor SiARDP binds to the dehydration-responsive element (DRE) of the SiLTP promoter to activate its transcription [144].

Sterols are essential for the growth and sporulation of oomycetes [145], and elicitins, secreted by *Phytophthora* spp. and *Pythium* spp., can deliver sterols to oomycetes by scavenging them from synthetic liposomes and plant plasma membranes. A tobacco LTP1 was found to compete with the elicitin cryptogein from *P. cryptogea* for a common binding site on oomycetes, and this binding mitigated ROS accumulation caused by cryptogein [146]. *ScNsLTP* from sugarcane was found to be highly expressed at low temperature and in PEG treatment. However, its expression did not change upon *Sporisorium scitamineum* infection, indicating that *ScNsLTP* is more sensitive to abiotic challenge [147].

Brassica rapa nectar contains BrLTP2.1, a nsLTP with direct antimicrobial activity against *P. syringae* pv. tomato and antifungal activity against *T. viride*, *Bipolaris oryzae*, *Colletotrichum trifolii*, and *A. solani* [148]. The low IC_{50} values and the high concentration of BrLTP2.1 in nectar strongly suggest that BrLTP2.1 is secreted into the nectar to protect *Brassica rapa* from bacteria and fungi attack [148]. ABA treatment induces the accumulation of ABA and LTP in phlo-em cells and root suberization in pea plants, and molecular modeling and fluorescence spectroscopy confirm that Ps-LTP1 can bind ABA, suggesting the involvement of plant LTPs in ABA transport in stress responses[149]. Xue et al. reported that 238 nsLTP genes in rapeseed (*Brassica napus*) were randomly distributed in the rapeseed genome, and their RNA-seq analysis showed that the expression of nsLTP genes were tissue-specific and were involved in response to various stresses (e.g., drought, heat, salinity, and cold), phytohormones (IAA and ABA), as well as in the phytopathogenic fungi attack (*Sclerotinia sclerotiorum*), white stem rot and *Leptosphaeria maculans*, blackleg) [150]. Among the 72 *nsLTP* genes that responded to white stem rot disease, 4 genes *BnLTP033*, *BnLTP129*, *BnLTP161*, and *BnLTP264* might have a major function in resistance to this disease, meanwhile *BnLTP161* and *BnLTP015* may play important role in plant defense against blackleg. The inhibitory effect of nsLTPs on microbial growth remains largely unknown, however, previous studies suggested that nsLTPs might increase cell permeability, leading to the disruption of structure of the cell membrane.

7.2. The use of plant non-specific lipid transfer protein genes in transgenic plant development

Overexpression of *TaLTPIb.1*, *TaLTPIb.5*, or *TaLT-PId.1* in Arabidopsis promoted longer roots and faster growth in chilling conditions, which suggests that these genes played a supportive role in improving chilling tolerance [143]. In a study by Julke and Ludwig-Muller (2016), overexpression of *LTP1* and *LTP3* in transgenic Arabidopsis enhanced salt stress tolerance[151]. The study also observed a reduction in clubroot susceptibility, which is caused by the obligate biotrophic protist *Plasmodiophora brassicae*, in *LTP3* transgenic Arabidopsis plants [151]. However, this study contrasted with Gao et al.'s study, which found that overexpression of LTP3 increased susceptibility to *P. syringae* pv. tomato[152]. These contradictory results indicate that the defensive functions of LTPs may vary between different pathogens. The accumulation of LTPs was observed in the phloem tissue of pea (*Pisum sativum* L.) under salinity stress, which implies the formation of water-impermeable barrier or the transport of phloem signaling [153]. In other studies, SiLTP was found to localize in the cytoplasm [144], while TaLTP3 signal was mainly detected in the cell membrane [154]. Due to their important roles in various developmental and physiological processes, mediation, and manipulation of nsLTPs expression are promising ways to increase plant resistance to different types of stress [155]. A heat-responsive gene *Lipid Transfer Protein 3 (TaLTP3)* from wheat (*T. aestivum* L.) involved in the response to salinity, drought, ABA, and heat stress [154]. The *TaLTP3* transgenic Arabidopsis plants exhibited higher heat tolerance than the control plants at the seedling stage [154]. It is evident that TaLTP3 confers heat stress tolerance via ROS scavenging mechanism, thereby reducing the accumulation of H_2O_2 and membrane injury caused by heat stress [156]. Similarly, the overexpression of *TdLTP4*, a LTP gene from durum wheat (*Triticum turgidum* L. subsp. Durum Desf.), maintained plant growth in salinity, H_2O_2, ABA, and JA treatments [157]. The enhanced resistance to oxidative stress would be explained by the accumulation of ABA that facilitated ROS scavenging in plant cells. In addition, the detached leaf assay revealed that leaves from the *TdLTP4* transgenic Arabidopsis line expressed an enhanced resistance against *A. solani* and *B. cinerea* [156]. Tobacco seeds expressing *SiLTP* had higher germination ratios than the WT on the medium supplemented with 100 mM NaCl, 200 mM and 250 mM mannitol [144]. In addition, the *SiLTP* transgenic tobacco plants had longer roots and shoots than the WT plants on 100 mM NaCl or 200 mM mannitol treatment [144]. The tobacco expressing SiLTP also had greater proline and soluble sugar contents than those in the WT under drought and salinity conditions. This implies the ectopic activity of SiLTP enhanced plant tolerance to abiotic stress. In a report by Gangadhar et al. (2016), *StnsLTP1* transgenic potato plants exhibited enhanced cell membrane integrity, reduced lipid peroxidation, and hydrogen peroxide, compared to non-transgenic plants under heat, drought, and salt stress conditions [158]. An increase in the accumulation of ascorbates and in the expression of defensive genes *StCAT*, *StAPX*, *StSOD*, *StHsfA3*, *StsHSP20*, and *StHSP70* were observed in the *StnsLTP1* transgenic potato plants. These results infer that the *StnsLTP1* plants tolerated better to abiotic stress through the scavenging of ROS by enhanced antioxidant enzyme activities [158]. The transgenic wheat Bobwhite and RB07 lines carrying an overexpressed *AtLTP4.4* gene demonstrated inhibitory effects on the growth of *F. graminearum* in the greenhouse and minimized fungal lesion size in leaf assays [31]. Moreover, the accumulation of deoxynivalenol (DON), a virulence factor of *F. graminearum*, was noticeably decreased in the *AtLTP4.4* transgenic Bobwhite lines [31].

Table 1. PAMPs-based Transgenic Plants.

Gene	**Origin**	**Transgenic organisms**	**Promoter**	**Targeting pathogens or abiotic agents**	**Transformation method**	**References**
			Thionins			
α-thionin	Barley (*Hordeum vulgare* L.)	Tobacco (*N. tabacum* L.)	*CAMV35S*	*P. syringae* pv. *tabaci* 153 *P. syringae* pv. *syringae*	Leaf-disc infection	Carmona et al. (1993) [159]
β-purothionin	Wheat (*T. aestivum* L.)	*A. thaliana*	*Carbonic anhydrase (CA)* promoter	*P. syringae* strain DC3000 *F. oxysporum* f. sp. *matthiolae*	Vacuum infiltration method	Oard and Enright (2006) [53]
Hordothionin	Barley (*H. vulgare*)	Apple (*Malus domestica*)	*CaMV35S*	*P. syringae* pv. *tobacco* *P. syringae* pv. *syringae*	*Agrobacterium tumefaciens* AGL0	Krens et al. (2011) [160]
α-hordothionin	Barley (*H. vulgare* L.)	Sweet potato (*Ipomoea batatas* (L.) Lam.)	*E12Ω*	*Ceratocystis fimbriata*	*A. tumefaciens*	Muramoto et al. (2012) [55]
Modified thionin (*Mthionin*)	Citrus (*Citrus* L.)	Carrizo citrange	Double *35S* (*D35S*)	*Candidatus* Liberibacter asiaticus (Las) *Xanthomonas citri*	*Agrobacterium tumefaciens* EHA105	Hao et al. (2016) [58]
Modified thionin (*Mthionin*)	*A. thaliana*	*A. thaliana*	Double *35S* (*D35S*)	*Fusarium graminearum*	*Agrobacterium*-mediated floral dip method	Hao et al. (2020) [59]
Thio-60 and *Thio-63*	*A. thaliana*	*Paulownia tomentosa*	*SP6*	*E. carotovora* *Pseudomonas aeruginosa*	Chitosan nanoparticles	Hussien (2020) [161]
Thio-60	*A. thaliana*	Onion (*Allium cepa* L.)	*SP6*	*A. niger*	Chitosan nanoparticles	Tawfik et al. (2022) [49]
Thio-60	*A. thaliana*	Date palm (*Phoenix dactylifera* L.)	*SP6*	*F. oxysporum*	Chitosan nanoparticles	Allah et al. (2023) [61]
Defensins						
OsDEF7, *OsDEF8*	Rice (*O. sativa* L.)	*Rosetta-gami E. coli* (DE3)	*Tac*	*Xanthomonas oryzae* pv. *oryzae* *X. oryzae* pv. *oryzicola* *E. carotovora* subsp. *atroseptica*	Not mentioned	Tantong et al. (2016) [162]
AtPDF1.1	*A. thaliana* Col-0	*A. thaliana*	*CAMV35S*	*Pectobacterium carotovorum* subsp. *carotovorum*	*Agrobacterium*-mediated floral dip method	Hsiao et al. (2017) [78]
Ca-AFP	Chickpea (*Cicer arietinum* L.)	*A. thaliana*	*CAMV35S*	Water-deficit stress	*Agrobacterium*-mediated floral dip method	Kumar et al. (2019) [34]
ZmDEF1	Maize (*Zea mays* L.)	Maize (*Z. mays* L.)	*pBetaPhaso*	*Sitophilus zeamais* Motsch	*A. tumefaciens* C58	Vi et al. (2019) [163]
PnDEFL1	*Panax notoginseng*	*A. cepa* L., *N. tabacum* L.	*CaMV35S*	*Fusarium solani* *F. oxysporum* *Botrosphaeria dothidea* *S. sclerotiorum*	*A. tumefaciens* EHA105	Wang et al. (2019) [164]

PtDef	*Populus trichocarpa*	*Populus trichocarpa*	*CAMV35S*	*Septotis populiperda*	*A. tumefaciens* EHA105	Wei et al. (2019) [165]
MsDef1	*Medicago sativa*	*N. tabacum*	*M24*	*P. aeruginosa* *R. solanacearum* *Xanthomonas campestris* *A. niger* *Pyricularia oryzae* *R. solani* *P. syringae* pv *tabaci*	*A. tumefaciens* GV3850	Deb et al. (2020) [166]
CAL2	Rice (*O. sativa* L.)	*O. sativa* L. var. ZH11, *A. thaliana*	*CAMV35S*	Cadmium detoxification	*Agrobacterium*-mediated floral dip method	Luo et al. (2020) [89]
α-TvD1	Shrub (*Tephrosia villosa* (L.) Pers)	*N. tabacum*	*CAMV35S*	*Phytophthora parasitica* var. *nicotianae* *A. alternata* *R. solani* *Spodoptera litura*	*A. tumefaciens* LBA4404	Sharma et al. (2020) [167]
Chitinase I, defensin	*Solanum tuberosum chitinase I, Vigna radiata defensin*	Tea (*Camellia sinensis* L.)	*CAMV35S*	Blister blight (*Exobasidium vexans*)	*A. tumefaciens* LBA4404	Singh et al. (2020) [168]
NmDef02	*Nicotiana megalosiphon*	Soybean (*Glycine max* L.)	*CAMV35S*	*Phakopsora pachyrhizi* *Colletotrichum truncatum*	Bombardement	Soto et al. (2020) [169]
pgDEF	*Panax ginseng*	*A. thaliana*	*CAMV35S*	*F. solani*	*A. tumefaciens* AGL0	Sun et al. (2021) [170]
Tfgd2-RsAFP2	*Impatiens balsamina* L.	Pigeonpea (*Cajanus cajan* (L.) Huth)	*CAMV35S*	*H. armigera*	*A. tumefaciens* EHA105	Nalluri and Karri (2023) [171]
NaD1	*Nicotiana alata*	*N. tabacum* cv. Xanthi tobacco	*CAMV35S*	Drought stress	*A. tumefaciens* GV3101	Royan et al. (2023) [87]
RsAFP2	Radish (*Raphanus sativus* L.)	Chickpea (*C. arietinum*)	*CAMV35S*	*F. oxysporum* f. sp. *Cicero*	*A. tumefaciens* LBA4404	Sadhu et al. (2023) [172]
Hevein-like antimicrobial peptides						
Pn-AMP1, Pn-AMP2	*Pharbitis nil* L.	Tobacco (*N. tabacum*)	*CAMV35S*	*Phytophthora parasitica*	*A. tumefaciens* EHA101	Koo et al. (2002) [118]
Pro-SmAmp1	Chickweed (*Stellaria media*)	*A. thaliana*	*CAMV35S*	*B. cinerea* *B. sorokiniana*	*A. tumefaciens* AGL0	Shukurov et al. (2010) [173]
AMP1, AMP2	Chickweed (*S. media*)	Tomato (*S. lycopersicum* L.)	*CAMV35S*	*Phytophthora infestance*	*A. tumefaciens* AGL0	Khaliluev et al. (2011) [121]
Pro-SmAMP1, Pro-SmAMP2	Chickweed (*S. media*)	Tobacco (*N. tabacum*) cv. Samsun-NN, *A. thaliana* Col-0	*CAMV35S*	*B. sorokiniana* *Thielaviopsis basicola*	*A. tumefaciens* AGL0	Shukurov et al. (2012) [174]
Pro-SmAmp2	Chickweed (*S. media*)	Potato (*S. tuberosum* L.) var. Yubiley Zhukova	*CAMV35S, pro-SmAMP2*	*Alternaria* spp. *Fusarium* spp.	*A. tumefaciens* AGL0	Vetchinkina et al.

						(2016) [175]
Hevein-like gene	not mentioned	Asparagus (*Asparagus officinalis* L.) var. Jing Kang 701	*CAMV35S*	*Phoma asponaqi* Sacc	*A. tumefaciens* EHA105	Chen et al. (2019) [176]
Pro-SmAmp1	Chickweed (*S. media*)	Potato (*S.tuberosum* L.) var. Zhukovsky ranny and Udacha	*CAMV35S*	*A. alternata* *Alternaria solani*	*A. tumefaciens*	Beliaev et al. (2021) [177]
Cyclotides						
Oak1 (kalata B1), asparaginyl endopeptidase	*O. affinis*	*Nicotiana benthamiana*	*CAMV35S*	*In planta kalata B1* production	*A. tumefaciens* LBA4404	Poon et al. (2018) [178]
Systemins						
Pro-systemin cDNA	not mentioned	Tomato (*S. lycopersicum* L.)	*CAMV35S*	Systemic signal propagation proteinase inhibitor accumulation	*A. tumefaciens* LBA4404	McGurl et al. (1994) [179]
Pro-systemin cDNA	not mentioned	Tomato (*S. lycopersicum* L.) cv. Red Setter	*CAMV35S*	*Macrosiphum euphorbiae*) *B. cinerea* *A. alternata* *Spodoptera littoralis*	*A. tumefaciens* C5851	Coppola et al. (2015) [180]
Pro-systemin cDNA	not mentioned	Tomato (*S. lycopersicum* L.)	CAMV35S	Cucumber mosaic virus, Necrosis satRNA, Non-necrogenic mutant "NNmut-satRNA"	*A. tumefaciens* LBA4404	Bubici et al. (2017) [181]
Pro-systemin cDNA	Tomato	*A. thaliana* Col-0	Shoot- or root-specific promoter, *CAMV35S*	*B. cinerea*	*Agrobacterium*-mediated floral dip method	Zhang et al. (2018) [128]
Truncated pro-systemin CDNA	Tomato	Tomato (*S. lycopersicum* L.) cv. Red Setter	*CAMV35S*	*Spodoptera littoralis* *B. cinerea*	*A. tumefaciens* C5851	Molisso et al. (2022) [182]
Non-specific lipid transfer protein genes						
Ace-AMP1	*Allium cepa*	Rice	*PAL* *maize ubiquitin (UbI)*	*R. solani* *Xanthomonas oryzae* *Magnaporthe grisea*	Bombardment, *A. tumefaciens* LBA4404	Patkar and Chattoo (2006) [183]
TaLTP3	Wheat (*T. aestivum* L.) cv. Chinese Spring	*A. thaliana*	*CAMV35S*	Heat stress	*Agrobacterium*-mediated floral dip method	Wang et al. (2014) [154]
TaLTPIb.1, TaLTPIb.5, TaLTPId.1	Wheat	*Nicotiana benthamiana*	*CAMV35S*	Cold, drought, wounding	*Agrobacterium*-mediated transformation	Yu et al. (2014) [143]
TdLTP4	Durum wheat (*T. turgidum* L. subsp. Durum Desf.)	*A. thaliana*	*CAMV35S*	*A. solani* *B. cinerea*	*Agrobacterium*-mediated floral dip method	Safi et al. (2015) [184]
StnsLTP1	Potato (*S. tuberosum* L.)	Potato (*S. tuberosum* L.)	*Double 35S (D35S)*	Heat, water deficit, salt stress	*Agrobacterium*-mediated transformation	Gangadhar et al. (2016) [158]

SiLTP	Foxtail millet (*Setaria italica*) cv. Jigu11	*A. thaliana* Col-0	*SiLTP* endogenous promoter	Salt and drought stress	*Agrobacterium*-mediated transformation	Pan et al. (2016) [144]
NtLTP4	Tobacco (*N. tabacum* L.)	Tobacco (*N. tabacum* L.)	*CAMV35S*	Salt and drought stress	*A. tumefaciens*-mediated leaf disc	Xu et al. (2018) [185]
GmLtpI.3	Soybean cv. Zhonghuang 39	Soybean cv. Williams 82, *Arabidopsis*	*CAMV35S*	Salt and drought stress	*Agrobacterium*-mediated transformation	Zhang et al. (2022) [186]
NtLTPI.38	Tobacco (*N. tabacum*)	Tobacco (*N. tabacum*) cv. K326	Not mentioned	Heat stress	*Agrobacterium*-mediated transformation	Song et al. (2023) [187]
AT14A	*A. thaliana* Col-0	Tomato (*S. lycopersicum* L.) cv. Yaxin 87-5	*CAMV35S*	Drought stress	*Agrobacterium*-mediated transformation	Xin et al. (2023) [188]

8. Conclusion

From the agricultural standpoint, most studies on PAMPs have focused on their antifungal and antibacterial potentials. Previous studies have also indicated that PAMPs might play crucial roles in regulating plant responses to abiotic stress. However, there is a significant need for a large volume of evidence to elucidate mechanisms underlying the involvement of PAMPs in abiotic stress response. This evidence should encompass molecular features, signaling pathways, interactions between PAMPs signaling and other phytohormones, as well as greenhouse and in-field tests to assess the effects of PAMPs. Thus far, published studies and known properties of PAMPs bode well for developing biocontrol substances through direct spray or transgenic approach. Nevertheless, the utilization of PAMPs-based elicitors to induce plant tolerance to abiotic stress demands additional efforts. Bridging this gap of knowledge is imperative to provide insights into the mechanisms of induced abiotic stress tolerance in crop plants using these elicitors, thereby bolstering our crop productivity amidst rising environmental challenges. Furthermore, the release of bioactive compounds to the environment from genetically modified crops has raised concern for both human health and the environment. The well-established stability of PAMPs suggests that these peptides could be highly persistent in soil and water. Consequently, a comprehensive assessment of the fate of PAMPs in soil and water, their interaction with other soil components, and their degradation is essential.

Author Contributions: Conceptualization, T.T.M.N, D.M.H.-T and C-CH; Writing-Original draft: T.T.M.N, D.M.H.-T, BVT, S-HWH, and C-CH; Supervision: C-CH. All authors have read and agreed to the published version of the manuscript.

Funding: This work received no external funding.

Informed Consent Statement: Not applicable.

Data Availability Statement: Not applicable.

Acknowledgments: We would like to express our gratitude to Dr. Tan Phong Nguyen, Faculty of Environment and Labour Safety, Ton Duc Thang University, Vietnam, and Dr. Nhuan Nghiem, Department of Environmental Engineering and Earth Sciences, Clemson University, Clemson, South Carolina, USA for helping us find the latest papers used in this work.

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

Abbreviation

ABA, abscisic acid; A. alternata, Alternaria alternata; APX, Ascorbate peroxidase; A. thaliana, Arabidopsis thaliana; B. cinerea, Botrytis cinerea; CAT, catalase; E. carotovora, Erwinia carotovora; F. oxysporum, Fusarium oxysporum; HypSys, Hydroxyproline-rich systemins; JA, Jasmonic acid; MIC, Minimum inhibitory concentration; N. tabacum, Nicotiana tabacum; O. sativa, Oryza sativa; PAL, Phenylalanine ammonia lyase; PAMPs: plant-derived antimicrobial peptides; P. infestans, Phytophthora infestans; PR, Pathogenesis-related; P. syringae, Pseudomonas syringae; R. solanacearum, Ralstonia solanacearum; R. solani, Rhizoctonia solani; S. aureus, Staphylococcus aureus; S. lycopersicum, Solanum lycopersicum; S. tuberosum, Solanum tuberosum; SOD, Superoxide dismutase; S. sclerotiorum, Sclerotinia sclerotiorum; T. aestivum, Triticum aestivum; T. turgidum, Triticum turgidum.

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