



Review

The use of versatile plant antimicrobial peptides in agribusiness and human health



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ABSTRACT

Plant immune responses involve a wide diversity of physiological reactions that are induced by the recognition of pathogens, such as hypersensitive responses, cell wall modifications, and the synthesis of antimicrobial molecules including antimicrobial peptides (AMPs). These proteinaceous molecules have been widely studied, presenting peculiar characteristics such as conserved domains and a conserved disulfide bond pattern. Currently, many AMP classes with diverse modes of action are known, having been isolated from a large number of organisms. Plant AMPs comprise an interesting source of studies nowadays, and among these there are reports of different classes, including defensins, albumins, cyclotides, snakins and several others. These peptides have been widely used in works that pursue human disease control, including nosocomial infections, as well as for agricultural purposes. In this context, this review will focus on the relevance of the structural-function relations of AMPs derived from plants and their proper use in applications for human health and agribusiness.

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1. Introduction

Animals and plants share common elements in their defense processes against pathogens, including direct antimicrobial activities by synthesis of hydrolytic enzymes (chitinases, glucanases, proteinases and oxidases) [109] as well as antimicrobial peptides (AMPs) [13,53]. Furthermore, indirect innate immunity strategies have also been observed; these include some activities in host organisms, like the production of hydrogen peroxide or synthesis of host defense peptides (HDPs) that can cause an immunomodulatory response [145]. AMPs have been isolated from a wide number of sources, including animals, bacteria and plants [73]. In a general perspective, these molecules can be organized into four large groups: (1) linear α -helical peptides; (2) cyclic peptides with β -sheet structures with two or more disulfide bonds; (3) a combination of helices and β -sheets stabilized by disulfide bonds; (4) peptides with β -hairpin or looped arrangement containing disulfide bonds; (5) linear peptides with an unusual predisposition for particular repetition of some amino acid residues, including proline, glycine, tryptophan or histidine and (6) short peptides with coil structures or with no defined secondary structures [128]. AMPs have been long described as components of the plant defense arsenal, regulating defense barriers or responses mainly activated by direct infections [53,109]. Most AMP families described for plants are cysteine-rich (4–8 Cys residues), with their globular structures being stabilized by disulfide bonds (S–S) that provide a high structural stability; among these are defensins and snakins [13]. AMPs can share similar properties, such as their small size (approximately 10 kDa), positive charges and high hydrophobic residues portion. These properties provide the possibility to fold into an amphiphilic structure with distinct hydrophobic and positively charged amino acid residues. Despite these general characteristics, some exceptions can also be observed, such as peptides smaller than 10 kDa and others with anionic charges [94,109]. Families of plant AMPs have been classified based on their homologies at the primary structural level [15,109] as well by the pattern mainly provided by disulfide bond pattern and structural scaffold [109]. In accordance with such properties, several classes of plant AMPs have been identified, including defensins, knottin-like, 2S albumins, cyclotides, lipid transfer proteins (LTPs), heveins and snakins. In addition to a vast structural diversity, plant AMPs also have a broad spectrum of activity against bacteria, fungi and viruses [109]. The mode of action of AMPs has been under continuous review, and in general peptide functions vary from membrane permeabilization to a complex intracellular signaling, also acting with immuno-modulatory activities [128].

1.1. Plant AMP classes

1.1.1. Defensins

The first plant defensins were isolated from wheat and barley and were called γ -thionins, due to their molecular masses of 5 kDa and the presence of four disulfide bonds, a pattern also found in α - and β -thionins. However, it was then discovered that γ -thionins were structurally different from α - and β -thionins, being then called defensins [98]. Defensins constitute an important class of antimicrobial peptides with a highly conserved structural scaffold, and they have been isolated from different organisms such as insects, mammals and plants [154]. In general, defensins have three to five disulfide bonds (Fig. 1A),

which stabilize an antiparallel β -sheet conformation flanked by an α -helical segment generating a compact structure that confers resistance toward extreme pH, temperatures and protease-mediated degradation [7,15,154]. Moreover, plant defensins are mainly small, cationic peptides of 45–54 amino acids in length, which have typically been isolated from seeds, but can also be found in other plant tissues such as leaves, flowers, roots and stems [80,81]. Commonly, their tridimensional structure consists of triple-stranded antiparallel β -sheets and one α -helix lying in parallel with the β -sheet. They are stabilized by four disulfide bonds, which incorporate the cystine-stabilized $\alpha\beta$ (C $\alpha\beta$) motif (C¹X_nC²X₃C³X_nC⁴X_nC⁵X₁C⁶) [53,153]. The C $\alpha\beta$ motif can also be found in defensins and toxins from other organisms such as insects and scorpions, respectively [80,82]. Interestingly, two defensins, named PhD1 and PhD2, isolated from *Petunia hybrida*, showed a different structural pattern, presenting one extra disulfide bond, which seems to replace a conserved hydrogen bond network that is present in the classical four-disulfide-bond plant defensins (C¹X_nC²X_nC³X_nC⁴X₃C⁵X_nC⁶X_nC⁷X₁C⁸) [120]. Among their functions, plant defensins are known to manifest a wide array of biological activities, such as antifungal [104] and antibacterial [38], and they also act on protein translation [27] and enzyme inhibition [53,98].

The first antifungal plant defensins described and characterized were two isoforms named *Raphanus sativus* antifungal protein 1 (*Rs*-AFP1) and *R. sativus* antifungal protein 2 (*Rs*-AFP2), which were isolated from radish (*R. sativus* L.) seeds [157] (Table 1). *Rs*-AFP1 and *Rs*-AFP2 are basic peptides stabilized by disulfide bonds with 35–43 amino acid residues length (5 kDa) arranged in oligomeric quaternary organization [157]. When evaluated against different fungi, *Rs*-AFP1 and *Rs*-AFP2 were able to inhibit *Pyricularia oryzae*, *Phoma betae* and *Cercospora beticola* (Table 1) [157]. Since then, several studies have been done in order to purify attractive new proteinaceous compounds from plants for therapeutic or agricultural purposes. Years later, the primary structure of the cowpea (*Vigna unguiculata*) defensin II (Cp-thionin II) was described [48]. Cp-thionin II is a monomeric peptide of 47 amino acids in length, molecular mass of 5.2 kDa and four disulfide bonds, which presents high similarities with known defensins. Cp-thionin II was further evaluated against both Gram-positive and -negative bacteria, revealing remarkable bactericidal activities against *Staphylococcus aureus*, *Escherichia coli* and *Pseudomonas syringae* (Table 1) [48]. Additionally, Fujimura et al. [50] purified two antimicrobial defensins, named *Fa*-AMP1 and *Fa*-AMP2, from buckwheat (*Fagopyrum esculentum* Moench.) seeds. *Fa*-AMP1 and *Fa*-AMP2 are also monomeric, cysteine-rich peptides consisting of 40 amino acid residues and molecular masses of approximately 4 kDa [50]. These peptides were active also against fungi such as *Fusarium oxysporum* and *Geotrichum candidum* (Table 1) [50]. The same authors also showed that two other monomeric defensins, *Pp*-AMP1 and *Pp*-AMP2, from Japanese bamboo shoot *Phyllostachys pubescences*, have antimicrobial activities against several plant-pathogenic bacteria and fungi (Table 1) [49].

Furthermore, Lay et al. [82] structurally characterized, for the first time, a plant defensin from *Nicotiana glauca* flowers named NaD1. NaD1 is a cysteine-rich, cationic peptide of 47 amino acids residues in length, which presents a pattern of conserved residues such as Ser⁷, Glu²⁷, Gly³², Phe¹⁰ and Gly¹² [82]. Electrostatically, NaD1 is characterized by a predominant cationic β -sheet and a neutral α -helix. Moreover, it is known that NaD1 acts as a proteinase

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