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Review Article

Antimicrobial Peptides with Plant Origin

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Abstract: According to the World Health Organization plants are one of the best sources to obtain a huge variety of biologically active compounds. Human population during centuries has used plants and plants extracts in ethno medicine to cure wide range of diseases. In the scope of modern methods of isolation and purification of different plant substances, antimicrobial peptides (AMPs) give us the opportunity to have a new ally in the fight with different microbial pathogens. Possible future uses of AMPs derived from plants could be either as a new class of anti-infective medications or as bio-preservatives in foods and beverages.

Keywords: Plant AMPs, Antimicrobial Action, AMPs Properties

1. Introduction

Plants have been used for centuries as a valuable source of natural products for maintaining human health and infections control. Today, microbial infections pose a significant health problem all over the world and plants may become part of the solution because they are rich in antimicrobial agents. According to the World Health Organization (WHO) medicinal plants would be the best source to obtain a huge variety of active compounds. One kind of these compounds that plants produce is small cysteine-rich antimicrobial peptides (AMPs). They are one of the mechanisms of natural defense which may be expressed constitutively or induced in response to a pathogen attack. Plant AMPs are released immediately after infection is initiated. They are expressed as a single gene and therefore require less biomass and energy consumption [1, 2].

Plant AMPs are small cationic peptides with molecular masses of 2–10 kDa. Their structures are stabilized through formation of 2-6 disulfide bridges. Plant AMPs belong to several classes and their classification is based on different properties and functions:

i. with coded gene and non-gene coded. The scientists are focused on the gene coded, but some non-ribosome synthesized peptides are used in the medicinal practice as antibiotics (collistin);
ii. with different biological functions: The activities of plant AMPs are primarily directed against fungal, oomycete-, and bacterial microorganisms, but certain representatives of this class can be directed against other targets, including herbivorous insects [3, 4, 5];
iii. based on the physico-chemical peptide properties such as charge, hydrophobicity, length, amphipathicity and solubility. The net charge of known AMPs, which is the sum of all charges of ionizable groups of the peptide, varies from negative to positive and it is the main factor for the initial interaction with negatively charged cell membranes. By changing the net charge of an AMP, its

antimicrobial and hemolytic activities can be altered to achieve selective killing of microbes with no or minimized effects on host cells. Hydrophobicity has also been shown to influence the activity and selectivity of AMP molecules. Almost 50% of amino acids in the primary sequence of natural AMPs are hydrophobic residues. In most cases, the increase of the hydrophobicity on the positively charged side of an AMP (below a threshold) can increase its antimicrobial activity, while the decrease of the hydrophobicity can reduce its antimicrobial activity. The size for an AMP to transverse the lipid bilayer of bacteria in the barrel-stave model should be at least 22 amino acids for *α*-helical AMPs, while eight amino acids are needed for β-sheet AMPs. Besides the effects of length on its 3D structure and mode of action, the length of an AMP may also affect its cytotoxicity. Amphipathicity is another important property of AMPs to ensure their activity and interaction with microbial membranes. It is shown that amphipathicity is more important than hydrophobicity for binding to microbial membranes. Because amphipathicity of AMPs is required for a strong partition into the membrane interface, priority should be given to the amphipathic structure when designing synthetic AMPs for specific target cells. Since AMPs should act on or enter through lipid membranes, they need to be soluble in aqueous environments. If AMP molecules aggregate, it will lose its ability to interact with the cell membrane [6]. On Table 1 are shown examples of AMPs isolated from different wide spread plants.

iv. based on covalent bonding pattern: This universal classification system (UC) categorizes antimicrobial peptides (or peptide in general) into four classes [7, 8]:
a. Class UCLL: linear one-chain peptides or two linear peptides not connected via a covalent bond;
b. Class UCSS: sidechain-sidechain linked peptides (e.g. disulfide-containing defensins). A sidechain-sidechain connection can occur within a single peptide chain or between two different peptide chains;
c. Class UCSB: polypeptide chains with a sidechain to backbone connection;
d. Class UCBB: circular polypeptides with a peptide bond between the N- and C-termini (i.e., backbone-backbone connection). This structure has been found for cyclotides from plant AMPs;

v. based on 3D structure AMPs are classified into four families: *α*-, *β*-, *αβ*-, and non-*αβ*-depended on the types of secondary structures. The alpha family consists of AMPs with helical structures. The beta family is composed of AMPs with beta-strands. While the alpha beta family comprises both helical and beta-strands in the 3D structure, the non-alpha beta family contains neither helical nor beta-strands;

vi. based on the molecular targets AMPs can be divided in cell surface targeting peptides and intracellular targeting peptides. Cell surface-targeting peptides, including both membrane-targeting and non-membrane targeting peptides, can be further classified based on specific targets such as cell wall/carbohydrates, lipids/membranes, and proteins/receptors. Likewise, intracellular targeting AMPs can be further classified based on the specific target molecules (e.g. proteins, DNA, and RNA).

2. Plant Antimicrobial Peptides

2.1. Thionins

Thionins are one of the major groups of plant AMPs. The first thionin isolated from wheat endosperm was α-purothionin. These plant AMPs are known as plant toxins with antifungal and antibacterial activity. Expressions of thionins in plant tissues could be initiated by expose to different pathogens. Their proposed antinfective mechanism of action is interaction between thionins hydrophobic residues and the positively charged membranes of different foreign invaders. The proposed mechanism of toxicity is attributed to lysis of cell membranes, but it is still under investigation. The thionins are toxic to animal cells, presumably attacking the cell membrane and rendering it permeable: this results in the inhibition of sugar uptake and allows potassium and phosphate ions, proteins, and nucleotides to leak from cells [9]. Another proposed antimicrobial activity is disrupting the Calcium influx during certain cellular changes in the membrane polarity [10]. Berocall-Lobo et al. (2009) research showed that wheat thionin antibacterial activity against *Leishmania donovani*, was highest among plants AMPs. They collapsed calcium ionic and pH gradients across the parasite plasma membrane together with a rapid depletion of intracellular ATP without affecting mitochondrial potential. Hence the lethal effect of thionins was mostly associated to permeabilization of the plasma membrane leading to an immediate death of the parasite. *Leishmania* caused the visceral form of leishmaniosis known as kala-azar [11, 12].

Thionins are mainly found in seeds where they may act as a defense against consumption by animals. A highly toxic to plant pathogens thionin isolated from barley (*Hordeum vulgare*) leaf is involved in the mechanism of plant defense against microbial infections [13]. The hydrophobic protein crambin from the Abyssinian kale (*Crambe abyssinica*) is also a member of the thionin family [9]. Some thionins have cytotoxic activity and they are therefore interesting in the development of new drugs against cancer with novel action mechanisms [14].

The role of this natural defenses in the plants determines their division on the flower-specific (*Nicotiana alata, Nicotiana tabacum*); Gamma-thionins *Triticum aestivum* (Wheat) endosperm (gamma-purothionins); gamma-hordothionins *Hordeum vulgare* (Barley) which are toxic to animal cells and inhibit protein synthesis in cell free systems [15], antifungal proteins (AFP) (seeds of Brassicaceae species such as radish, mustard, turnip and *Arabidopsis thaliana* - Thale Cress) [16], inhibitors of insect alpha-amylases from sorghum [17], probable protease inhibitor P322 (*Solanum tuberosum* - Potato), a germination-related proteins (*Vigna unguiculata* - Cowpea)

[18], anther-specific protein SF18 from sunflower. SF18 is a protein that contains a gamma-thionin domain at its N-terminus and a proline-rich C-terminal domain, *Glycine max* (Soybean) sulfur-rich protein SE60 [19], *Vicia faba* (Broad bean) antibacterial peptides fabatin-1 and -2. Thionins from cereals and *Pyrularia pubera* have four disulfide bonds. Other dicotyledonous thionins have three disulfide bonds. The structural feature common to all thionins is the G (gamma) fold consisting of two antiparallel a-helices that form a stem and antiparallel b-sheets that form an arm [20]. A groove exists between the helical and b-sheet segments.

2.2. Defensins

Defensins are another group of derived from plants AMPs. They are the most studied representatives of this family. They are cationic peptides of 45-54 amino acids with four to five disulfide bonds. Plant defensins have diverse biological functions which include antifungal and antibacterial properties. [21-24]. The structure-function relationship of plant defensins has been suggested to correlate with their positive charge and amphipathic nature. That suggestion lie on the theory that, plant defensins could initially bind to microbial membranes through interactions with specific binding sites ("receptors"), as reported for Rs-AFP2, Hs-AFP1, and Dm-AMP1. Binding of plant defensins, such as Rs-AFP2 and Dm-AMP1, to the cell membrane results in the influx and efflux of positive ions like Ca^{2+} and K^{+}. Lastly, Ms-Def1 is able to block the Ca^{2+} channel in a manner similar to the Ca^{2+} channel blocker KP4. It was demonstrated that NaD1 does not cause membranes permeabilization via a canonical mechanism which involves nonspecific insertion into membranes but rather a cell wall dependent process, likely requiring a specific receptor. The mechanism of the fungicidal action of NaD1 is likely through permeabilization of the hyphae of *Fusarium oxysporum*, entering into the cytoplasm of the cell and inducing ROS oxidative stress. Also the high-osmolarity glycerol (HOG) pathway is involved in the protection of the cell against NaD1, indicating that the inhibition of the HOG pathway increases the activity of antimicrobial peptides against *Candida albicans* [25].

Hevein and hevein-like peptides are first isolated from *Hevea brasiliensis*. Due to their high glycine content and conservative lectin domeins they have high bonding ability to the chitin layer of the chitin-containing fungi, therefore inhibiting their growth [26].

2.3. Plant Lipid Transfer Proteins

Plant lipid transfer proteins are quite abundant and comprise of two families, LTP1 and LTP2. Members of the plant LTP1 family are about 10 kDa in size, consist of 90-95 amino acids, and are basic, with isoelectric points between 9 and 10. These LTPs have eight Cys residues conserved at similar positions in their primary structure, which form four disulfide bridges stabilizing the tertiary structure [27]. The LTP2 family members share the properties of the LTP1 family but are only about 7 kDa in size, possessing about 70 amino acids on average. LTPs contain a signal peptide at the amino terminal end, which is cleaved and targets the mature peptide to the cellular secretory pathway resulting in export to the apoplast.

The classes of plant AMPs described above are the most commonly used by plants as defensive mechanism. They show a constitutive pattern of expression with up regulation in response to pathogen attack, injury and some abiotic stresses. Ke et al. (2015) researched the ability of *Brassica napus* genes to respond to microbial invasion. They used BLASTX and Blast2GO programs and found that 28 recombinant AMPs displayed antimicrobial activities against *E. coli* and *Micrococcus luteus* and *Sclerotinia sclerotiorum* strains [28]. Proline-rich antimicrobial peptide was identified again from *B. napus* from Cao et al. (2015). Up to now, they have been reported in some insects, vertebrate and invertebrate animals, but are not found in plants. The peptide exhibited strong antimicrobial activity against Gram-positive bacterium, Gram-negative bacterium, yeast and also had strong antifungal activity against several pathogenic fungi, such as *Sclerotinia sclerotiorum*, *Mucor sp*., *Magnaporthe oryzae* and *Botrytis cinerea* [29]. Other researchers also report inhibitory effects of peptides from prickly ash seed on *Escherichia coli*, *Salmonella*, *Bacillus subtilis*, and *Staphylococcus aureus*. Authors suggest that antimicrobial activity of these peptides increases in a dose-dependent manner. They retained sufficient antibacterial activity at pH values between 2.0 and 12.0 [30]. Peptides isolated from *Artemisia alba* inhibited the growth of *Listeria monocytogenes*, *Staphylococcus aureus*, *Bacillus cereus* and *Bacillus cytotoxicus*. According to the scientists the peptides are stable up to 10 minutes heating at 120°C and they resisted organic solvent effects, therefore they are suitable for food bio-preservation as natural additives or in human infectious disease treatments against multi-drug resistant pathogens [31]. Astafieva et al. purified and determined the amino acid sequences of three novel antimicrobial peptides: ToAMP1, ToAMP2 and ToAMP3 from *Taraxacum officinale* flowers. The peptides are cationic and cysteine-rich and active against fungal and bacterial pathogens, and therefore represent new promising molecules for biotechnological and medicinal applications [32].

Snakins are one of the most recent AMPs that have been discovered in Solanaceae family. They induce the aggregation of both Gram-positive and Gram-negative bacteria and therefore, are recognized as components of constitutive and inducible plant defense barriers. These antibacterial properties are mostly due to Snakin-1 and Snakin-2 isolated from potatoes tuber [33, 34].

3. Conclusion

Antimicrobial peptides have been described in many different plant species. They belong to a wide range of protein families. Most peptides are able to inhibit the activity of both Gram-positive and Gram-negative bacteria and different fungi species. Proposed mechanism of their actions is well described in most research and review articles. Parameters such as

aggregation and permeabilisation of the pathogen's membranes are essential for the anti-infective action of plant derived AMPs. Another future role of those peptides could be as bio-preservatives, because some of the described species exhibit the strength and stability that are needed in order one substance to be researched further as a potential preservative. Need of those is crucial in the modern world, because of the numerous reports that chemically made conservants are one of the major reasons of allergies and pathogen resistance. Further scientific work is needed in both fields but plant AMPs hold great promise for the future.

Table 1. *Sequence, sources, properties and activity of AMPs, isolated from plants [35].*

Name	Sequence	Source	Net charge	Hydrophobic residue %	Activity
Hispidalin	SDYLNNNPLFPRYDIGNVELSTAYRSFANQKAP GRLNQNWALTADYTYR	Winter melon seeds, *Benincasa hispida*	+1	30	antibacterial, antifungal, antioxidant
Kalata B1	GLPVCGETCVGGTCNTPGCTCSWPVCTRN	African herb, *Oldenlandia affinis*	0	37	antibacterial, antiviral, insecticidal, anti-HIV, enzyme inhibitor
Cycloviolacin O3	GIPCGESCVWIPCLTSAIGCSCKSKVCYRN	*Viola odorata*	+2	46	antiparasitic
Ah-AMP1, defensin	LCNERPSQTWSGNCGNTAHCDKQCQDWEKAS HGACHKRENHWKCFCYFNC	Horse chestnuts, *Aesculus hippocastanum*	+1	34	antifungal
Ginkbilobin	ANTAFVSSAHNTQKIPAGAPFNRNLRAMLADL RQNAAFAG	*Ginkgo biloba*	+3	47	antifungal
Fabatin-1	LLGRCKVKSNRFHGPCLTDTHCSTVCRGEGYK GGDCHGLRRRCMCLC	Broad bean, *Vicia faba*	+6	36	antibacterial
S. oleracea defensin 1	TCESPSHKFKGPCATNRNCES	Leaves and stems, *Spinacia oleracea*	+1	23	antibacterial, antifungal
Griffithsin	SLTHRKFGGSSPFSGLSSIAVRSGSYLDAIIIDG VHHGGSGGNLSPTFTFGSGEYISNMTIRSGDYI DNISFETNMGRRFGPYGGSGGSANTLSNVKVI QINGSAGDYLDSLDIYYEQY	Red alga, *Grifithsia* sp.	-3	28	antiviral, anti-HIV

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