

## ANTIOXIDANT AND ANTIMICROBIAL PEPTIDES AS ADDITIVES IN ACTIVE AND BIODEGRADABLE FOOD PACKAGING: A REVIEW

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**Review**



**ABSTRACT**

The pervasive reliance on non-biodegradable plastics in food packaging poses significant environmental and public health challenges. This critical issue has promoted the development of sustainable alternatives, particularly bioplastics, which can be further enhanced into active packaging systems. This comprehensive review highlights the significant potential of antioxidant and antimicrobial peptides (AMPs) as key bioactive additives in this emerging field. Derived from diverse biological sources (animals, plants, microorganisms), these short amino acid sequences (typically 2-20 AAs) exhibit a broad spectrum of bioactivities, including potent antioxidant, antimicrobial, antiviral, and antidiabetic effects. Their effectiveness is rooted in diverse mechanisms such as free radical scavenging, metal chelation, and direct microbial membrane disruption, which collectively contribute to prolonging food shelf life and enhancing safety. The aim of this review is to provide an up-to-date perspective on the application, sources, and underlying mechanisms of antimicrobial and antioxidant peptides in active and biodegradable food packaging. While offering immense benefits for food preservation and sustainability, widespread adoption hinges on addressing critical challenges related to their long-term stability, cost-effective production, standardized regulatory frameworks, and consumer acceptance. Ultimately, advanced research in peptide extraction, synthesis, and formulation holds the key to unlocking their full potential and transforming the food packaging industry towards more secure and environmentally sustainable practices.

**Keywords:** bioplastics; food oxidation; bioactive peptides; peptide sequence

**INTRODUCTION**

Food packaging materials serve as a primary barrier to cover or wrap food, offering crucial protection against diverse factors such as oxidation reactions, microbial contamination, physical damage, heat, water vapor permeability, ultraviolet rays, and pressure. This protective role is paramount for the food industry, as it directly contributes to food quality and safety, ensures food security, mitigates environmental risks, and influences the consumer's initial perception (Montoya-Anaya et al., 2023; Rusková et al., 2023). Responding to growing consumer demand for biodegradable packaging capable of extending food product shelf life, new packaging technologies, including active packaging, have been developed. Active packaging involves agents designed to either release or absorb substances, broadly categorized into two types: 1) agents that do not migrate but absorb undesirable compounds from food (e.g., ethylene absorbers, moisture scavengers, and oxygen generators) and 2) agents that release active ingredients onto the food surface, playing a vital role in food preservation through antimicrobial and antioxidant properties (Núñez-Gastélum et al., 2019; Dirpan et al., 2023).

A key consumer demand is the reduction of chemical preservatives in food. In this context, active packaging methods utilizing peptides with antimicrobial or antioxidant properties have emerged as a significant technological advancement. Notably, countries such as Spain, Italy, and China are at the forefront of research in this area (Dirpan et al., 2023). Peptides are biomolecules defined as short chains of amino acids, typically comprising 2 to 20 amino acids linked by peptide bonds. These biomolecules play a crucial role in the innate immune system and are ubiquitous across all living organisms, including bacteria, plants, fungi, and mammalian cells (Liu et al., 2021). Furthermore, the Antimicrobial Peptides Database (APD3) indicates that peptides exhibit a remarkably broad spectrum of activities, encompassing antimicrobial, antioxidant, antiviral, antiparasitic, antifungal, anticancer, antidiabetic, antitoxin, spermicidal, anti-HIV, and antibiofilm properties.

A distinct and pressing problem stems from the pervasive use of non-biodegradable plastics in packaging, including common types such as PET, PP, and PS. Globally, a substantial 40% of all plastics produced are allocated for packaging, yet a meager 7% of these are recycled annually. In response to this environmental and resource challenge, various biodegradable plastics have been proposed as alternatives to conventional options. These include, for instance, polylactic acid (PLA), poly-β-hydroxybutyrate-co-β-hydroxyvalerate (PHBV), poly(butylene adipate-co-

terephthalate) (PBAT), poly(butylene succinate) (PBS), and polycaprolactone (PCL) (Pulikkalparambil et al., 2023). Furthermore, complementing these material advancements, Rodríguez-Núñez et al. (2023) reported that biopolymers such as alginate, cellulose, chitosan, agar, carrageenan, and more recently, fucoidan and ulvan, are considered among the most promising natural materials for developing sustainable biodegradable packaging. The responsible development and subsequent application of these biodegradable and active packaging materials are subject to stringent regulatory frameworks, such as the European Parliament and Council Regulation No. 1935/2004, which aims to ensure their safe and effective use for improved food preservation. Against this backdrop, the aim of this review is to provide an up-to-date perspective on the application of antimicrobial and antioxidant peptides in active and biodegradable food packaging, achieved through an exhaustive literature analysis.

**Conventional food packaging**

Food packaging is an essential step in the food distribution supply chain as it ensures the safety and quality of food from production to consumption, its main functions are to contain and protect food as well to provide information, product name, contents, ingredients, and expiration date through labeling (Singh et al., 2022). Packaging is classified as primary, secondary or tertiary; the first corresponds to a coating/film that has direct contact with food, so this type of packaging has a great impact on quality; the second covers food previously packaged by primary packaging; and the third refers to packaging that protects the product during the supply chain, handling, distribution and storage (Ahari and Soufiani, 2021).

The main materials used in food packaging are paper, paperboard, glass, aluminum, plastic and/or a combination of these materials. These materials are selected based on the intrinsic and extrinsic properties of the food, as well as the storage conditions, required shelf life, regulatory requirements, cost, and functional properties of the packaging material (barrier and protection), with plastics being one of the most widely used materials in this industry (Singh et al., 2022). The most common plastics used for food packaging are polyethylene (PE), polyethylene terephthalate (PET), polypropylene (PP), polystyrene (PS) and polyvinyl chloride (PVC), which account for more than 90% of total plastic production, but also for 50-70% of total plastic waste (Baghi et al., 2022). In addition, these plastics are associated with several problems, including

environmental problems (damage to marine species through suffocation, chemical pollution, entanglement and ingestion) and health problems (cancer, reproductive and respiratory problems due to ingestion and inhalation). As a result, biopolymers are increasingly being used to develop biodegradable packaging materials because they are safe and renewable (Sani et al., 2022).

**Biodegradable material for packaging**

Bioplastics, defined as biodegradable and/or bio-based materials, can be sourced from various raw materials, including cellulose, agro-industrial waste, and linen. Alternatively, they can be produced through biotechnological processes such as fermentation, where microorganisms like fungi and bacteria yield biomass suitable for bioplastic applications (e.g., bacterial cellulose and polyhydroxyalkanoates). Despite their environmental advantages, bioplastics currently constitute less than 1% of total global plastic production. In 2022, a reported production of 2.2 million tons saw Asia as the leading producer (41.4%), followed by Europe (26.5%) and North America (18.9%), with significantly lower contributions from South America (12.6%) and Oceania (0.5%). Projections indicate a substantial increase in bioplastics production, reaching an estimated 6.3 million tons by 2027 (European Bioplastics, 2023).

Within this rapidly evolving sector, nearly 1.1 million tons (48%) of annual bioplastics production are specifically dedicated to the packaging industry. However, bioplastics also find extensive applications across diverse sectors, including food service, consumer electronics, automotive, agriculture/horticulture, toys, and textiles. Of the global bioplastics output, biodegradable plastics such as PLA, PHA, and starch blends account for 51%, while the remaining portion consists of bio-based but non-biodegradable materials (e.g., PE, PTT, PA, and PP) (European Bioplastics, 2023).

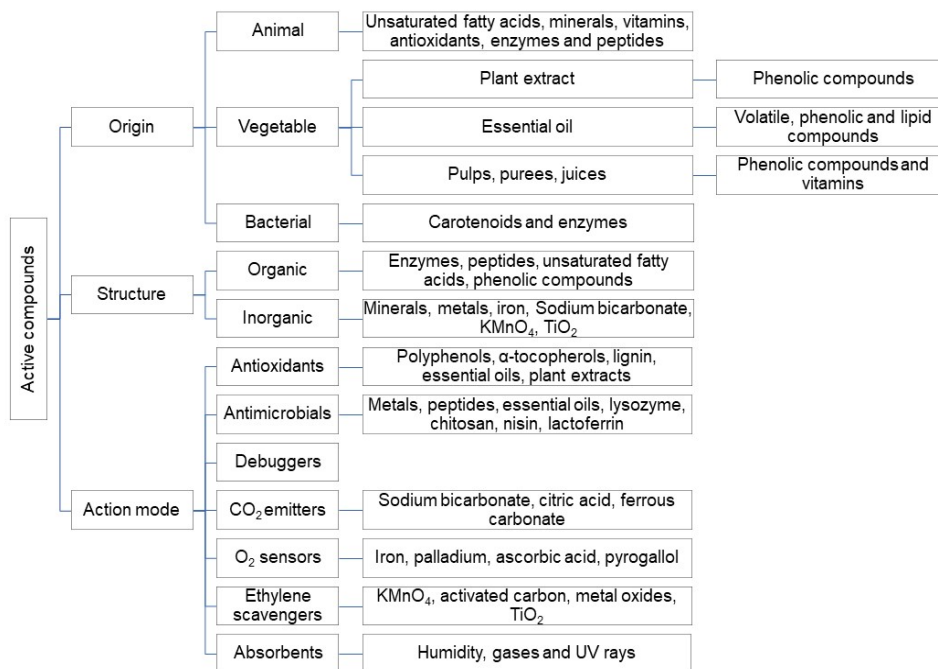
Beyond general bioplastics, other biodegradable biopolymers—such as polysaccharides, proteins, and lipids—are also explored for packaging and coating

applications in the food industry. Although their widespread use has been historically limited by suboptimal mechanical and barrier properties, significant advancements have been made through the development of polymer blends (Zhen et al., 2022). The integration of biopolymers into packaging systems offers numerous advantages, including inherent biodegradability, biocompatibility, sustainability, and non-toxicity. These renewable and environmentally compatible materials can effectively regulate the migration of water vapor, CO<sub>2</sub>, O<sub>2</sub>, and fats in foods, thereby contributing to extended quality and shelf life. Crucially, biopolymers also serve as excellent carriers for active functional ingredients (e.g., antimicrobials, antioxidants, and nutrients), facilitating the creation of truly biodegradable and active packaging systems (Sani et al., 2022).

**Active packaging**

The main functions of food packaging are to contain, communicate and protect food products; however, when it comes to quality, these functions are passive and insufficient, especially for highly perishable foods (Sánchez-Machado et al., 2015). In addition, constant changes in consumer preferences and demands have led to the development of new technologies in food packaging, smart packaging (indicators and sensors) and active packaging (bioactive substances incorporated into the packaging to preserve the quality of the food and extend its shelf life) (Singh et al., 2022).

The European Commission Regulation (EC) No 450/2009 defines active packaging as “packaging systems that intentionally contain components that would absorb or release substances since or into packaged food products or into the space surrounding them. The active compounds used in food packaging are classified according to different criteria: origin, structure, and mode of action, among others (Gil et al., 2023), as shown in Figure 1.



**Figure 1** Classification of active compounds used for active packaging. **Source:** Own elaboration.

Within this context, various botanical sources—including leaves, branches, roots, stems, peels, and seeds—are recognized as promising reservoirs of active compounds. These can be processed to yield extracts, essential oils, and diverse derivatives such as pigments, polyphenols, and peptides, all of which have been extensively investigated for their utility in food packaging systems, as detailed in Table 1. However, their practical application is often impeded by inherent

instabilities (e.g., thermal, oxidative, moisture, oxygen, and light sensitivity) during packaging manufacturing or subsequent product storage. Furthermore, plant extracts and essential oils can introduce undesirable sensory attributes, such as intense aroma and/or flavor (Mohd et al., 2023).

**Table 1** Active compounds used in food packaging systems

Compound	Polymer matrix	Packing food	Results	Author
Cinnamon	PLA and PBAT incorporated with TiO <sub>2</sub>	Cheese	Antimicrobial activity against <i>S. aureus</i> and <i>E. coli</i>	Sharma et al. (2023)
Mixture of carvacrol and eugenol (80:20) in β-cyclodextrin	Kraft paper sheets	Lemon	Increase the nutritional content of the pulp and the antioxidant activity of the flavedo tissue of lemon	López-Gómez et al. (2023)
Lemongrass and oregano	PLA and PHB	Strawberries	Showed antioxidant, antimicrobial and antifungal capacity	Rusková et al. (2023)
Cloves (30%)	PHB incorporated with nanosilica	Brown bread	Antibacterial activity against <i>E. coli</i> , <i>S. aureus</i> and <i>A. niger</i>	Mittal et al. (2023)

Watermelon peel extract	(0.5, 1, 1.5 and 2%) Chitosan and guar gum	Banana	Increase in DPPH radical scavenging activity (up to 83.24%), and antibacterial activity.	Wang et al. (2023a)
Scallion flower	Chitosan and esterified chitin nanofibers	Banana	Increased antibacterial capacity (1.9 times higher) and strong DPPH (74.8%) and ABTS (84.06%) radical scavenging activity	Xie et al. (2023)
Piper betel leaf (5 and 10% w/w)	PLA	Tuna meat	Excellent antioxidant (80.2%) and antimicrobial properties (18.05 and 16.05 mm against <i>S. aureus</i> and <i>E. coli</i> , respectively)	Radhalakshmi et al. (2023)
Kiwi peel (0.5, 1 and 1.5%)	Watermelon peel pectin	Chicken thighs	Excellent free radical scavenging activity, effective delay of lipid oxidation in the thighs	Han and Song, (2021)
Grape and pomegranate	PLA	Almonds and beef	High antioxidant capacity, in beef delay lipid oxidation and reduce microbial growth of <i>S. aureus</i>	Andrade et al. (2023)
Flavonoids: Catechin, quercetin and luteolin	Chitosan	Chilled meat	Increase in antioxidant capacity, inhibition of the growth of <i>L. monocytogenes</i> , <i>S. typhimurium</i> , <i>E. coli</i> y <i>S. aureus</i>	Sutharsan et al. (2023)
Oily tomato extract (lycopene and beta carotene)	Gelatin	None*	Improvement significantly antioxidant activity of the gelatin films.	López-Palestina et al. (2019)

Sources of bioactive peptides

Bioactive peptides can be derived from various sources, primarily through the enzymatic hydrolysis of plant and animal proteins or through fermentation methods. Notably, plants have demonstrated a rich content of bioactive peptides that can enhance the shelf life of foods when integrated into active packaging (Rivera-Pino et al., 2023). However, Santos et al. (2018) pointed out that isolating pure natural peptides from these sources often results in low yields and high costs, posing challenges for industrial applications. Consequently, the chemical synthesis of analogous bioactive peptides is gaining popularity, offering advantages such as lower costs, improved stability, higher purity, and reduced toxicity. In this context, Narsi et al. (2022) reported that submerged and solid-state fermentation are effective methods for obtaining bioactive peptides from microorganisms. These processes utilize microorganisms' own enzymes for protein hydrolysis (proteolytic activity), eliminating the need for external proteases and significantly reducing costs. Furthermore, the antimicrobial peptides (AMPs) produced through lactic acid fermentation using food-grade lactic acid bacteria, such as *Lactobacillus* spp., *Lactococcus* spp., *Streptococcus* spp., and *Bifidobacterium* spp., are likely to be among the most rapidly regulated antimicrobial peptides in the food industry due to their safe origins (Cotter et al., 2005).

Antimicrobial peptides for active packaging

Antimicrobial peptides are widely recognized for their effectiveness as antimicrobial agents due to their broad capacity to target a variety of microorganisms, including bacteria, fungi, yeasts, and even viruses (Rodríguez-Sánchez et al., 2023). Cotto et al. (2005) highlighted that bacteriocins—AMPs produced by bacteria—obtained through lactic fermentation provide promising opportunities for developing innovative food preservation technologies. These peptides are heat-stable and exhibit activity against a range of bacteria, particularly gram-positive ones, though their efficacy against gram-negative bacteria generally requires damage to the outer membrane. AMPs are effective at low concentrations, exhibit rapid antimicrobial actions, and are less likely to induce resistance compared to traditional antibiotics (Luo et al., 2023; Chowdhury et al., 2024). Their mechanism of action involves interaction with bacterial cell membranes, leading to the formation of pores. Moreover, AMPs can penetrate the cells and destabilize DNA and RNA by binding to active sites. Typically, these peptides consist of 15 to 45 amino acids (Dirpan et al., 2023) and can be classified based on their charge into cationic or anionic peptides. Cationic peptides usually contain 10 to 100 amino acids and possess a net charge ranging from +2 to +9, whereas anionic peptides consist of 5 to 70 amino acids with a net charge from -1 to -8 (Savitskaya et al., 2023). Table 2 provides an overview of the current applications of AMPs in active food packaging.

Table 2 Current applications of AMPs in active and biodegradable food packaging

AMPs/source	Formulation of packaging	Results	Author
Synthetic peptide (Palindromic peptide LfcinB (21–25) <sub>pal</sub> )	Polycaprolactone with nanofibers of pullulan loaded with the peptide (multilayer system)	Antimicrobial effect against <i>Escherichia coli</i> (MIC = 15 µM)	Rodríguez-Sánchez et al. (2023)
Peptide HX-12C (synthetic peptide)	Chitosan films loaded with the peptide	Antimicrobial effect against <i>Escherichia coli</i> and <i>Staphylococcus aureus</i> . Even the coating in fresh pork meat controlled the total viable counts until the 20th day of storage	Luo et al. (2023)
Synthetic peptides: Lfcin-β, MBP-1, and PLGG. The peptides LL37, Cys-LL37, melittin, RW4 and nisin were purchased. Three Apolipoproteins B were synthesized ((r(P)ApoB <sub>L</sub> <sup>Pro</sup> , r(P)ApoB <sub>S</sub> <sup>Pro</sup> and r(P)ApoB <sub>L</sub> <sup>Ala</sup> )) based from host defense peptides in humans	Coating of chitosan, furcellaran and carp skin gelatin hydrolysate with 8 different active peptides	Coatings of stored pork ham and pork loin. The coating with the peptides RW4 and LL37 were the most effective against <i>Aspergillus flavus</i> and decreasing the total viable count (3.5 log cfu/g)	Kulawik et al. (2023)
Commercial nisin and carvacrol	Coating chitosan with the r(P)ApoB <sub>S</sub> <sup>Pro</sup> peptide on polystyrene surfaces	2.5 µM of r(P)ApoB <sub>S</sub> <sup>Pro</sup> significantly decreased the biofilms production of <i>Salmonella typhimurium</i> ATCC® 14028 and <i>Salmonella enteritidis</i> 706 RIVM	Dell’Olimo et al. (2021)
Pediocin and nisin in nanoclays of halloysite	The bioplastic mater-bi was used as biodegradable and compostable option	The combination of nisin and carvacrol showed significant antibacterial activity against <i>Listeria monocytogenes</i> , <i>Salmonella enteritidis</i> , <i>Escherichia coli</i> , and <i>Staphylococcus aureus</i> .	Lopresti et al. (2021)
	Packaging based on starch-halloysite nanocomposites	The packaging showed antimicrobial activity against <i>Listeria monocytogenes</i> and <i>Clostridium perfringens</i> . However, <i>Listeria monocytogenes</i> was more sensible to these peptides	Meira et al. (2017)

Antioxidant peptides in active packaging

Bioactive peptides are fragments of 2 to 50 amino acid units encoded in proteins from various natural sources (plants, animals, fungi, microorganisms and their derivatives) that can be released by enzymatic proteolysis and are capable of exerting positive physiological/biological effects; antioxidant, antimicrobial, antihypertensive, anticancer, anti-aging and anti-inflammatory effects, among others; these effects are determined by several factors, such as the degree of

hydrolysis, the enzyme/substrate ratio, the substrate concentration, the physicochemical conditions (pH, temperature), the microorganism used, the incubation time, the molecular weight and the hydrophobicity (Rivero-Pino et al., 2023). Synthetic antioxidant peptides used in the food industry and related fields, such as butylated hydroxyanisole (BHA) and butylated hydroxytoluene (BHT), may pose potential health risks, which is why natural antioxidant peptides have gained popularity as they have been shown to be safe and have good antioxidant capacity

that can extend the shelf life of foods (Wang et al., 2021); however, techniques such as microencapsulation are required to protect them, as peptide uptake is easily affected by environmental factors, including light, humidity, temperature, and pH, which limits their applications (Li et al., 2023). Although plants are an abundant source of antioxidant peptides, they are not currently used in the food industry because the antioxidant capacity of these

peptides is reduced or even lost after hydrolysis or free AA. However, many of these plant peptides have demonstrated antioxidant activity when used as hydrolysates and protein isolates (Zou et al., 2016; Rivero-Pino et al., 2023). Table 3 shows the use of different sources (hydrolysates/isolates/natural protein concentrates) of antioxidant peptides in food packaging systems.

**Table 3** Sources of antioxidant peptides and their use in food packaging systems

Source	Biopolymer	Packaged food	Results	Author
Hydrolyzed of pine fruit protein (amino acids: arginine, glutamic acid, leucine, among others)	Oxidized bacterial nanocellulose	Pacific white shrimp	It presented antioxidant and antimicrobial properties; it was effective in preventing deterioration and inhibiting oxidation	Pirveisi et al. (2023)
Wheat germ protein isolate	PLA/ ethyl cellulose	None	Better antioxidant activity, reduced the growth of gram-negative bacteria ( <i>E. coli</i> ) and gram-positive bacteria ( <i>S. aureus</i> )	Hosseini et al. (2023)
Protein hydrolysates from soybean bran	Furcellaran	Butter	Increased the antioxidant capacity, the film did not extend the shelf life of the butter but behaved in the same way as synthetic films	Jamróz et al. (2022)
Alanine-Tyrosine synthetic antioxidant peptide	Carp skin gelatin hydrolyzed and furcellaran	Chilled Atlantic mackerel (fish)	Slowed lipid oxidation processes and inhibited the growth of microorganisms	Tkaczewska et al. (2021)
Shrimp and crab protein hydrolysates	Chitosan and fish gelatin	None*	Greater antibacterial and antioxidant potential	Hajji et al. (2021)
Microalgae protein concentrate ( <i>Spirulina platensis</i> )	Gelatin	Chilled fish	Lower counts were obtained for aerobic mesophiles, psychrotrophs, proteolytic, lipolytic and enterobacteria	Stejskal et al. (2020)
Cuttlefish protein hydrolysates	Cuttlefish skin gelatin	None*	Greater UV barrier and antioxidant potential	Kchaou et al. (2020)
Cotton seed hydrolysates	Alginate	None*	Increased total phenolic content and antioxidant activity, inhibited the growth of <i>S. aureus</i> , <i>C. gloeosporioides</i> and <i>R. oligosporus</i>	de Oliveira et al. (2019)
Soy, corn, and casein peptides	Chitosan	None*	Casein peptides showed the highest antibacterial activity and radical scavenging activity	Li et al. (2020)
Brewer's spent grain protein	Spent grain protein film	None*	Antimicrobial properties against <i>B. cereus</i> , <i>S. Newport</i> and <i>P. corylophilum</i> and antioxidant capacity	Proaño et al. (2020)

\*None: Peptides were not applied in foods, they were only tested *in-vitro*.

**Characteristics of antioxidants and antimicrobial peptides**

The functionality of peptides is largely influenced by their unique structural characteristics, as summarized in Table 4. Factors such as the type, composition, sequence, specific positioning of amino acids within the chain, as well as the overall length of the peptide, play crucial roles in determining their antioxidant and antimicrobial activities (Nwachukwu and Aluko, 2019; Wen et al., 2020). Most AMPs contain basic amino acids (AAs) in their primary sequences, including lysine (Lys), arginine (Arg), alanine (Ala), leucine (Leu), phenylalanine (Phe),

tryptophan (Trp), isoleucine (Ile), tyrosine (Tyr), and valine (Val). Some AMPs may also feature repeated sequences of these AAs. Nearly 50% of these peptides are hydrophobic and tend to exhibit high cationic charges, ranging from +2 to +11, making them more active than peptides with neutral or negative net charges (Wang et al., 2021). Additionally, AMPs are characterized by properties such as good thermal stability, water solubility, straightforward structure-activity relationships, and low sensitivity to environmental changes (Lei et al., 2019).

**Table 4** Characteristics of the peptides with antioxidant and antimicrobial capacity

Characteristics	Antioxidants		Antimicrobials	
	General	Amphipathic	General	Amphipathic
AAs units	5-16		12-50	
Molecular weight	< 3kDa		< 10kDa	
Structure	Secondary	$\alpha$ helices and $\beta$ sheets	Secondary (aqueous solutions)	Not defined
			Secondary (membrane level)	$\alpha$ helices (most common), $\beta$ sheets and cyclics
Source	<i>In vivo</i> digestion, <i>in vitro</i> enzymatic hydrolysis, fermentation, and germination		<i>In vitro</i> by enzymatic hydrolysis	

Source: Zou et al. (2016); López-García et al. (2022)

In contrast, antioxidant peptides predominantly consist of anionic AAs, alongside a high proportion of hydrophobic AAs (such as histidine (His), tryptophan (Trp), phenylalanine (Phe), proline (Pro), glycine (Gly), lysine (Lys), isoleucine (Ile), leucine (Leu), and valine (Val)). They also feature aromatic AAs (Trp, Tyr, His, and Phe) and sulfur-containing AAs (methionine (Met) and cysteine (Cys)), which may confer some antimicrobial properties as well. Met and Cys are particularly notable for their high ferric ion reducing antioxidant power (FRAP), while AAs like Trp, Tyr, His, Phe, Ala, Leu, and Pro demonstrate exceptional free radical scavenging activity through direct electron transfer. Anionic AAs, such as glutamic acid (Glu) and aspartic acid (Asp), are effective DPPH radical scavengers and can

also reduce metal cations due to their ability to provide excess electrons (Nwachukwu and Aluko, 2019).

The imidazole ring of His is capable of participating in single-electron transfer reactions and hydrogen atom transfer (HAT), enhancing its metal chelation and radical scavenging capacity. Meanwhile, the indole ring of Trp and the pyrrolidine of Pro function as hydrogen donors through their -OH groups, acting as scavengers of hydroxyl (-OH) radicals. Other AAs, including Lys, Gly, Val, and Ile, contribute to forming a hydrophobic microenvironment that favors the activity of peptide molecules (Zou et al., 2016; Nwachukwu and Aluko, 2019). An overview of these peptides can be found in Tables 5 and 6.

**Table 5** Sources and AA sequences of the antioxidant peptides

Source	Enzymes	Sequence of AAs	Function	Author
Sweet apricot seed	Alcalase	SHNLPILR and SEAGVTE	-O <sup>2-</sup> anion and -OH radical scavenging activity and Fe chelating capacity	Huang et al. (2022)
	Neutrase	KVPIRVF, VAPTAVK, FDLPVDSEHK, GRQVIHAVK and GIGTSIGVTK	Relatively high DPPH radical scavenging activity	
Cricket ( <i>Gryllus bimaculatus</i> ) protein fractions	Alcalase (Glutelin)	TEAPLNPK, EVGA, KLL, TGNLPGAAHPLLL, AHLLT, LSPLYE, AGVL, VAAV, VAGL and QLL	High ABTS radical scavenging activity and metal chelating activity	Fashakin et al. (2023)
Silver carp muscle hydrolyzate	Alcalase Papain	VKVGNEF MEAPPH	High free radical scavenging activity	Wang et al. (2023b)
<i>Moringa oleifera</i> seeds	Pepsin	FLSeML, LSeMAAL, LASEMMVL, SeMLLAA and LSeMAL (with selenium)	Excellent DPPH and ABTS radical scavenging activity	Che et al. (2023b)
Peanut Hydrolysates ( <i>Arachis hypogaea</i> )	Pepsin	PGCPST	High antioxidant capacity and elimination of -OH radicals	Ma et al. (2023)
Pearl shell meat hydrolysate ( <i>Pinctada martensii</i> )	Protease neutrase	SPSSS, SGTAV and NSVAA	DPPH and ABTS radical scavenging activity and binding to antioxidant enzymes (CAT and SOD) and antioxidant channel proteins (Keap1)	Huang et al. (2023)
Sesame protein	Alcalase and trypsin	SYPTECRMR	High DPPH and ABTS radical scavenging capacity	Lu et al. (2018)
Wheat germ protein hydrolysates	Pepsin	KELPPSDADW	High radical scavenging activity ABTS	Karami et al. (2019)

**Table 6** Sources and AA sequences of antimicrobial peptides

Source	Peptide	Length	AAs sequence	Function	Author
Pine needles of <i>Pinus densiflora</i> Sieb. and Zucc.	PN5	11	FKFLARTGKFL	Active against gram-positive bacteria ( <i>S. aureus</i> , <i>L. monocytogenes</i> and <i>B. subtilis</i> ), gram-negative bacteria ( <i>E. coli</i> , <i>S. typhimurium</i> , <i>P. aeruginosa</i> and <i>A. baumannii</i> ), anti-inflammatory, antiseptic and antibiofilm	Lee et al. (2021)
<i>Zataria multiflora</i>	Dendrocin-ZM1	33	TTLRLNTLAY KVAWLNVK AFWAAGRAL KKVGR KVGRHLVKG	Active against <i>S. aureus</i> ATCC 25923, <i>E. coli</i> ATCC 25922, resistant <i>S. aureus</i> ATCC43300, VRSA <i>S. aureus</i> and <i>E. coli</i> ATCC35218	Seyedjavadi et al. (2022)
Hot peppers, interspecific hybrid ghost pepper <i>Capsicum chinense</i> × <i>frutescens</i>	CC-AMP2	37	LGKIFRAGKV IFCNTCKTCN GLCDYCCA	Active against <i>E. coli</i> ATCC 25922	Culver et al. (2021)
	CC-AMP1	32	QETLDPICMA KCVLKCGKK AWCLTKCIAG CVL	Active against gram-negative bacteria <i>E. coli</i> ATCC 25922, <i>K. pneumoniae</i> VK148, <i>A. baumannii</i> 5075 and <i>P. aeruginosa</i> 1423	
Legume <i>Medicago truncatula</i> .	NCR169	38	EDIGHIKYCGI VDDCYKSKK PLFKIWKCVE NVCVLWYK	Antimicrobial activity against <i>E. coli</i> and <i>S. meliloti</i>	Isozumi et al. (2021)
<i>Zea mays ssp. mexicana</i>	SM-985	21	GAGIGPGHRR TWRWRPRRR WR	Active against gram-positive bacteria ( <i>C. fangii</i> , <i>C. michiganensis</i> ssp. <i>Michiganensis</i> and <i>B. subtilis</i> 168) and gram-negative bacteria ( <i>E. coli</i> BL21, <i>R. solanacearum</i> , <i>X. campestris</i> pv. <i>holcicola</i> , <i>X. oryzae</i> pv. <i>oryzae</i> and <i>P. syringae</i> pv. <i>tomato</i> DC3000)	Qutb et al. (2020)
<i>Clitoria ternatea</i>	Cter G	30	GLPCGESCVFI PCITTVGCSI CKNKVCYNN	Active against <i>E. coli</i> , <i>P. aeruginosa</i> , <i>S.aureus</i> and <i>C.albicans</i>	Strömstedt et al. (2017)

**Action mechanisms of antioxidant peptides**

Currently, the antioxidant capacity of peptides can be evaluated by in vivo animal methods, in vitro cell biology methods, and chemical methods, and the main mechanisms of action of the latter include (1) removal of reactive oxygen free radicals; (2) chelation of metal ions; and (3) inhibition of lipid peroxidation reactions (Zhu et al., 2022). Elimination of reactive oxygen free radicals: Antioxidant peptides can scavenge free radicals by two main mechanisms: homolytic or hydrogen atom transfer (HAT) and single electron transfer (SET). Peptides with Tyr residues mainly perform their function through HAT. The antioxidant techniques of free radical scavenging (TRAP), oxygen absorbance capacity (ORAC), carotene bleaching (Wen et al., 2020), crocin bleaching (CBA), and lipid peroxidation (LPA) use HAT as the mechanism of action to measure the antioxidant capacity to eliminate free radicals (Zou et al., 2016). Antioxidant peptides with Cys, Trp and His residues act primarily by the SET mechanism. Assays generally classified as SET reactions include Trolox equivalent antioxidant capacity (TEAC), DPPH radical scavenging activity and copper II reduction capacity (CRC) assays, and ABTS radical scavenging activity

and ferric radical scavenging capacity (FRAP). It has been reported that both mechanisms can occur in tandem, but one may dominate more than the other depending on the structure of the peptide in terms of its systemic solubility, type of assay, and partition coefficient. Despite their differences, both mechanisms produce identical end products; moreover, the amino acid residues important for HATs are also important for SET (Zou et al., 2016; Zhu et al., 2022). Metal ion chelation: Antioxidant peptides use the following mechanisms to chelate metal ions: (1) donate hydrogen, which allows the original valence of metals to be maintained, in addition to preventing metal ions from catalyzing lipid oxidation; (2) block the formation of lipid peroxides by chelating metal ions via a transport mechanism, as these act as coenzymes during the Fenton reaction; and (3) block the lipid oxidation process by rendering the catalyst ineffective by forming complexes with the metal ion component of the enzymes. The main method used to evaluate the reducing capacity of Fe<sup>2+</sup> is the determination of the ferric reducing antioxidant power (FRAP) (Wen et al., 2020). Inhibition of lipid peroxidation reactions: Antioxidant peptides can inhibit lipid peroxidation in the following ways: (1) by inhibiting the production of reactive oxygen species (ROS) or scavenging active species that cause oxidative initiation;

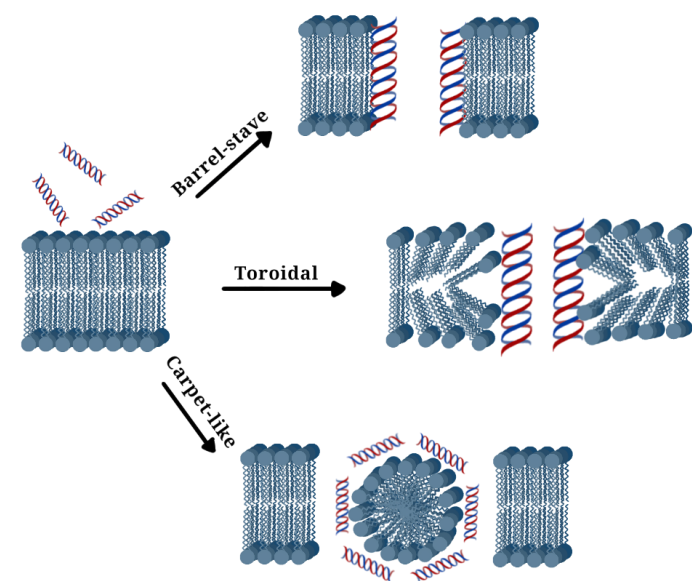
(2) by donating protons to lipid-derived lipid peroxide radicals (LOO•), a less reactive hydroperoxide is formed, thus stopping chain reactions; (3) their emulsifying properties provide them with unique inhibitory capacity (i.e., strong lipase inhibitory activity) and physical protection since this property allows them to adsorb to the surface of lipid molecules, creating a thick membrane that prevents direct contact between lipids and radicals. This property allows them to adsorb onto the surface of lipid molecules, forming a thick membrane that prevents direct contact between lipids and radicals with other oxidizing compounds; and (4) hydrophobic AAs increase the solubility of peptides in lipids, thereby promoting better interactions with free radicals. Lipid peroxidation assays include  $\beta$ -carotene/linoleic acid emulsion systems, thiobarbituric acid (TBARS), peroxide index, ferric thiocyanate, and electron spin resonance (Wen et al., 2020; Zhu et al., 2022).

### Action mechanisms of AMPs

AMPs exhibit diverse mechanisms of action, which are largely dictated by their intrinsic characteristics, including their amino acid sequence, amphipathic and secondary structure, and electrostatic charge (Figure 2). Furthermore, extrinsic factors such as peptide concentration and the lipid composition and conditions of microbial membranes significantly influence these mechanisms (Li et al., 2021; Chen and Jiang, 2023).

Most AMPs are predominantly cationic, a feature that drives their initial electrostatic attraction to the anionic cell membranes of both Gram-positive and Gram-negative bacteria. This attraction is primarily mediated by the negatively charged teichoic acids and lipopolysaccharides present in these bacterial cell walls, respectively (Luo and Song, 2021). Upon membrane contact, AMPs adopt amphiphilic structures: their hydrophobic domains interact with the hydrophobic core (i.e., the fatty acid tails of the lipid bilayer), while their cationic domains engage with the negatively charged hydrophilic phospholipid head groups.

At optimal concentrations, AMPs self-assemble within the cell membrane. This assembly leads to the formation of pores, often described by models such as the "toroidal pore" and "barrel-stave," or to the creation of micelles, characteristic of the "detergent" and "carpet" models. Both outcomes result in membrane permeabilization, causing leakage of vital ions and metabolites, disrupting osmotic regulation, and ultimately leading to cell rupture and lysis. Moreover, some AMPs can be translocated into the cytoplasm, where they engage with intracellular targets (Drayton et al., 2021).



**Figure 2** Proposed mechanisms of action for AMPs. **Source** Own elaboration.

**Carpet-like model:** in the carpet-like model, cationic AMPs initially bind to the bacterial membrane surface through electrostatic interactions. Their hydrophobic regions orient towards the membrane while hydrophilic regions face the solvent, effectively covering the surface. Upon reaching a critical threshold concentration, these AMPs penetrate and distort the membrane, forming micelles, which ultimately leads to cell lysis (Figure 2) (Ahmed and Hammami, 2019).

**Barrel-stave model:** in the barrel-stave model, AMPs insert vertically into the cell membrane's lipid bilayer, assembling like staves of a barrel to form transmembrane pores (Li et al., 2021). This mechanism unfolds in distinct steps: (1) AMPs, typically as monomers, initially bind to the membrane surface; (2) their cationic charge then induces the separation of polar phospholipid head groups, leading to localized membrane thinning that permits the hydrophilic region of the peptide to insert; and (3) peptide monomers subsequently self-aggregate and integrate into the membrane core, with their hydrophobic surfaces (e.g.,  $\alpha$ -helices or  $\beta$ -sheets) orienting outwards towards the acyl chains of the membrane (Figure 2). The

sustained accumulation of these peptide monomers leads to an expansion in pore size. This model is predominantly associated with highly hydrophobic peptides, particularly those comprising 20 or more amino acids, such as alamethicin (Ciurac et al., 2019).

**Toroidal pore model:** in the toroidal pore model, AMPs initially adsorb vertically onto the lipid bilayer surface, inducing structural transformations. This leads to membrane flexing and the formation of a pore composed of both peptides and phospholipids. Within this pore, the peptides form a core shell, maintaining permanent contact with the water core and the lipid head groups (Figure 2) (Seyfi et al., 2019; Ciurac et al., 2019). This mechanism is commonly associated with peptides like PGLa and magainin. Furthermore, it is also proposed for AMPs that target intracellular components, as pore disruption can facilitate their translocation into the cytoplasm (Ciurac et al., 2019). The toroidal pore model is considered an intermediate between the "carpet-like" and "barrel-stave" models. A key distinction from the barrel-stave model lies in the pore's internal arrangement: while both involve vertical insertion, in the toroidal model, the hydrophilic regions of both AMPs and lipid head groups are oriented towards the pore's aqueous interior, rather than AMPs interacting solely with lipid tails (hydrophobic regions) as in the barrel-stave model. Additionally, toroidal pores are generally transient and exhibit lower stability compared to those formed by the barrel-stave mechanism (Chen and Jiang, 2023). Furthermore, distinguishing from the carpet-like model, the toroidal pore creates well-defined transmembrane structures, whereas the carpet-like model results in a less defined array of surface-bound peptides (micelles) (Li et al., 2021).

**Targeting the cell wall:** certain AMPs, such as bacitracin and vancomycin, specifically inhibit bacterial cell wall synthesis by binding to lipid II. This crucial molecule is essential for the formation of peptidoglycan, the primary structural component of the bacterial cell wall (Luo and Song, 2021). Beyond this, Gram-positive bacteria notably feature teichoic and lipoteichoic acids within their cell walls, which serve as alternative targets for AMPs. For instance, AMPs like melittin and cecropin, known for their membrane-disrupting capabilities, also efficiently bind to these teichoic acids. This strong electrostatic attraction is due to the negatively charged phosphate groups present in teichoic acid structures (e.g., approximately 24 repeating glycerol phosphate units in *S. aureus*), which interact favorably with positively charged AMPs. However, it has been shown that cell lysis from membrane disruption only occurs when the bacterial cell membrane is completely saturated with AMPs (Malanovic and Lohner, 2016).

**Intracellular action:** beyond membrane disruption AMPs can exert their effects within bacterial cells once they successfully penetrate the membrane through mechanisms such as direct translocation or endocytosis. Upon entering the cytoplasm, AMPs can target essential macromolecules, including nucleic acids and ribosomes, thereby disrupting vital cellular processes. For instance, certain AMPs have been shown to bind to DNA and interfere with replication and transcription, leading to dysfunctional protein synthesis (Cardoso et al., 2019; Hwan et al., 2025). Additionally, studies reveal that AMPs can interact with bacterial ribosomal subunits, causing inhibition of protein translation (Li et al., 2021). Furthermore, a recent study demonstrated that specific AMPs can also induce the formation of reactive oxygen species (ROS) within bacterial cells, further impairing cellular functions and promoting cell death (Savitskaya et al., 2023). These multifaceted intracellular actions highlight the potential of AMPs as effective antimicrobial agents against resistant bacterial strains.

### CONCLUSION

The widespread use of non-biodegradable plastics in the food industry poses significant environmental and public health challenges, driving the search for sustainable and functional alternatives. This work highlights the great potential of antioxidant and antimicrobial peptides as key additives in the development of active and biodegradable food packaging. These bioactive peptides, obtained from diverse sources (animals, plants, microorganisms) and featuring well-characterized mechanisms of action—ranging from free radical neutralization and metal chelation to pore formation in bacterial membranes or interference with intracellular processes—offer a promising alternative to prolong food shelf life and enhance its safety. The incorporation of these bioactive peptides into packaging materials not only reduces reliance on chemical preservatives but also contributes to a more sustainable production and consumption model. However, for large-scale implementation, it is crucial to address challenges such as optimizing long-term stability and efficacy under real-world conditions, developing cost-effective production methods to ensure economic viability, establishing standardized regulatory frameworks to guarantee their safety for consumption, and promoting consumer acceptance. In summary, continuous research and development in the extraction, synthesis, and formulation of bioactive peptides is of vital importance. By overcoming these barriers, active packaging with peptides has the potential to revolutionize the packaging industry, offering innovative solutions that enhance global food security and reduce environmental impact.

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**Conflict of Interest** Authors declare that they have no conflict of interest.

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