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Mechanisms and applications of multifunctional low-temperature plasma technology for enhancing food safety

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ABSTRACT

Low-temperature plasma (LTP) is a promising green, non-thermal technology for food safety, addressing limitations of conventional methods that often compromise food quality. This review summarizes recent advancements in LTP applications, including microbial inactivation, mycotoxin degradation, pesticide residue reduction, and allergen mitigation. It also evaluates LTP's impact on food quality attributes such as color, texture, and nutrients, highlighting its potential benefits for consumer health. LTP-generated reactive species efficiently inactivate microorganisms, degrade toxins, and modify allergenic proteins. Compared to conventional techniques, LTP offers advantages of high efficiency, low temperature, and non-toxicity. The review discusses challenges and strategies for standardizing and scaling LTP technology, bridging research with industrial applications to promote sustainable green food processing for enhanced food safety.

1. Introduction

With the continuous development of the food industry, the growing consumer demand for food diversity has further heightened public concern regarding food safety. According to estimates by the World Health Organization (WHO), approximately 600 million people globally—equivalent to nearly 1 in 10 individuals—fall ill each year due to the consumption of contaminated food, with around 4.2×10^5 deaths resulting from foodborne diseases (Abed et al., 2025). The economic burden of unsafe food in low- and middle-income countries is significant, with annual losses in productivity and healthcare costs reaching approximately 1.1 billion USD (WHO, 2024). Furthermore, children under the age of 5 bear 40% of the global foodborne disease burden, resulting in an estimated 1.3×10^5 deaths annually (WHO, 2024). The U.S. Food and Drug Administration (FDA) estimates that the foodborne illness affects 48 million people annually in the U.S., resulting in 1.3×10^5 hospitalizations and 3000 deaths, and an estimated economic burden of $17.6 billion (Mosso et al., 2025).

Food safety hazards can be broadly categorized into chemical and biological types. Among them, chemical hazards-such as pesticide residues and heavy metal contamination-often enter the food chain through environmental exposure and are currently among the most concerning issues (Qin et al., 2021). Biological hazards include pathogenic microorganisms, spoilage microorganisms, mycotoxins, and food allergens. Spoilage microorganisms can cause substantial economic losses by deteriorating a wide range of food products (Pinu et al., 2016).

Abbreviations: LTP, low-temperature plasma; CD, corona discharge; DBD, dielectric barrier discharge; APPJ, atmospheric pressure plasma jet; GAD, gliding arc discharge; OH, hydroxyl radical; $^1O_2$, Singlet oxygen; O^{2-}, Superoxide anion; H_2O_2, Hydrogen peroxide; NO, Nitric oxide; $ONOO^-$, peroxynitrite; AFTs, aflatoxins; PUFAs, polyunsaturated fatty acids; LOOH, hydroperoxides; MDA, malondialdehyde; PCD, programmed cell death; -SH, thiol; Arg, Arginine; Pro, Proline; PI3K, phosphoinositide 3-kinase; PKB/Akt, Protein kinase B; mTOR, mechanistic target of rapamycin; DHA, docosahexaenoic acid; TPs, transformation products.

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Moreover, some spoilage organisms may act as opportunistic human pathogens, thereby posing additional challenges to food safety (Al-Kharousi et al., 2016). Fungal hazards, in particular, involve the damage caused by fungi and their mycotoxins (Tiwari et al., 2023). Mold can deteriorate food quality, and certain fungi produce toxins that pose serious food safety risks (Hudu et al., 2024). In addition, food allergens, mainly proteins, can trigger severe immune responses in sensitized individuals and may even be life-threatening (Costa et al., 2022).

Conventional approaches for contamination management commonly used in the food industry include thermal processing, such as pasteurization and sterilization, or freezing and refrigeration as low-temperature treatments, water activity control (through salting, sugaring, or drying), and the addition of chemical preservatives (Barba et al., 2017). Chemical treatments (e.g., chlorine/hypochlorite) can reduce produce marketability by promoting pigment loss/browning, altering flavor, and weakening texture (softening and water loss) (Rico et al., 2007). In addition, chlorine-based disinfection can react with dissolved organic matter to form potentially carcinogenic chlorinated disinfection by-products, such as trihalomethanes, thereby posing significant risks to human health and the environment (Li and Mitch, 2018). Additionally, although thermal processing methods are effective, they may cause significant chemical degradation, negatively affecting the sensory characteristics and adversely impacting the intrinsic qualities of treated foods (Ozen & Singh, 2020; Kadam et al., 2015). In recent years, researchers have explored various novel non-thermal processing technologies, such as high-pressure processing, pulsed light treatment, and ultrasound processing, aiming to ensure safety while preserving food quality as much as possible (Alanazi, 2023; Das et al., 2022; Liang et al., 2023). However, their high energy consumption may damage cellular structures and compromise texture stability and sensory acceptance. Therefore, the development of green, efficient, and mild multifunctional food processing technologies remains a key priority.

In recent years, LTP technology has emerged as a rapidly advancing non-thermal sterilization method in the food industry (Alaguthevar et al., 2024). LTP has been shown to reduce the total mesophilic aerobic bacteria by 0.4–1.4 log CFU/g and the total yeast and mold count by 0.7–2.7 log CFU/g in dried red pepper samples after 10 min of LTP treatment (Dikmetas et al., 2025; Shirazi et al., 2025). Additionally, under LTP treatment, maximal reductions in DON and OTA content were achieved after 8 min of exposure to cold plasma generated at 25 kV, resulting in reductions of 61.3 ± 2.4% and 55.6 ± 2.2%, respectively, in rice grains (Wang et al., 2020). Further studies have shown that LTP can reduce pesticide residues in various food matrices, including fruits and vegetables (Dong et al., 2025; Hsieh et al., 2025; Wang, Xing, et al., 2023). Under LTP treatment, the Ara h 1 content in hydrated peanuts decreased rapidly after air plasma treatment, with a 29% reduction observed after 30 min (Hsieh et al., 2025). Moreover, LTP helps preserve food quality by maintaining color, reducing darkening during storage, and causing no significant changes in food texture, with effectiveness depending on the food matrix and treatment conditions (Huang et al., 2025). Compared to conventional methods, LTP offers advantages such as lower operational costs, shorter treatment times at mild temperatures, non-toxicity, and broad applicability. However, further systematic research is needed to optimize and advance LTP technologies.

Although some reviews on LTP have been published in recent years, thereby advancing the understanding and application of LTP in food systems, existing syntheses have been focused on quality preservation and microbial inactivation; pesticide degradation mechanisms; fungal and mycotoxin control; as well as key nutrient impacts (Deng et al., 2025; Neuenfeldt et al., 2023; Rathod et al., 2021; Ravash et al., 2023; Shanker et al., 2023). However, a detailed review integrating LTP discharge configurations, reactive-species generation and characterization (short- and long-lived species), matrix-dependent effects, and the mechanisms of action in food safety together with associated quality and safety outcomes is still lacking in the available literature. In this review, recent advances in LTP for food processing are synthesized, with mechanistic evidence relevant to food-safety risk reduction being emphasized. The impacts of LTP on key quality attributes are evaluated, and potential consumer-relevant health implications are discussed in light of available toxicological and exposure evidence. Key elements required for safety assessment are summarized, existing evaluation approaches are compared, and major uncertainties requiring further validation are identified. Practical constraints and scale-up challenges are also outlined to inform broader adoption. This review is aimed at providing a theoretical basis for the industrial application of LTP technology in the food industry.

2. LTP technology and its advantages

The reactive species in LTP are initiated by external energy sources, such as electric fields, microwaves, or laser radiation. These external energy inputs cause gas molecules to ionize, generating free electrons, ions, and excited molecules (Tappi et al., 2016). These excited species are highly reactive and can undergo processes such as electron capture, ionization, and dissociation, further producing free radicals and other reactive species (Kopuk et al., 2022) (Table S1).

2.1. Principles of LTP technology

Plasma is recognized as the fourth state of matter, distinct from solids, liquids, and gases, composed of a mixture of charged and neutral particles while maintaining overall electrical neutrality (Pankaj et al., 2014). Plasma is formed when a gas absorbs sufficient external energy to undergo ionization. Based on the thermal equilibrium between electrons and heavy particles, plasmas are classified into thermal plasmas and LTP. LTP exhibits a non-equilibrium nature, with electron temperatures significantly higher than those of ions and neutral particles.

LTP can be further divided into quasi-equilibrium plasmas (operating at temperatures between 373.2 and 423.2 K) and non-equilibrium plasmas (cold plasmas, with temperatures below 333.15 K) (Saremnezhad et al., 2021; Tolouie et al., 2018). Cold plasmas are generated through gas discharge, with electron densities ranging from 10^9–10^{12} cm^{-3} and electron energies of 1–10 eV, while maintaining low gas temperatures (Mandal et al., 2018; Murtaza et al., 2024; Puligundla & Mok, 2020). The initiation of plasma discharge relies on collisions between electrons and gas molecules. Elastic collisions result in kinetic energy redistribution, whereas inelastic collisions transfer electron energy to the internal energy of molecules, triggering processes such as excitation and dissociation (Sanguansri et al., 2010; Surowsky et al., 2015; Xu et al., 2022). This generates highly reactive chemical species, such as ROS and RNS, which collectively drive various physicochemical reactions. This is one of the key reasons for the significant application potential of LTP in fields such as biomolecular dissociation and microbial inactivation (Shanker et al., 2023).

2.2. Generation methods of LTP

The generation of plasma requires an appropriate plasma system, which includes a carrier gas, a power supply, and electrodes. As shown in Fig. 1, discharge modes include corona discharge (CD), dielectric barrier discharge (DBD), atmospheric pressure plasma jet (APPJ), and glow discharge (GD).

CD typically exhibits a radially distributed discharge region and employs a sharp needle-tip or thin wire electrode. When the applied electric field is sufficiently strong and the energy gained by electrons reaches the ionization potential of gas molecules, corona discharge is initiated in the vicinity of the sharp electrode, as shown in Fig. 1A. CD is generally generated at atmospheric pressure and can produce a denser, higher-energy plasma than DBD, while offering operational simplicity and relatively low cost (Saremnezhad et al., 2021). In a CD plasma system operated at 2.0 A, the initial microbial loads on kumquats were reduced by 0.8–1.0 log CFU/g, and no noticeable changes in sensory

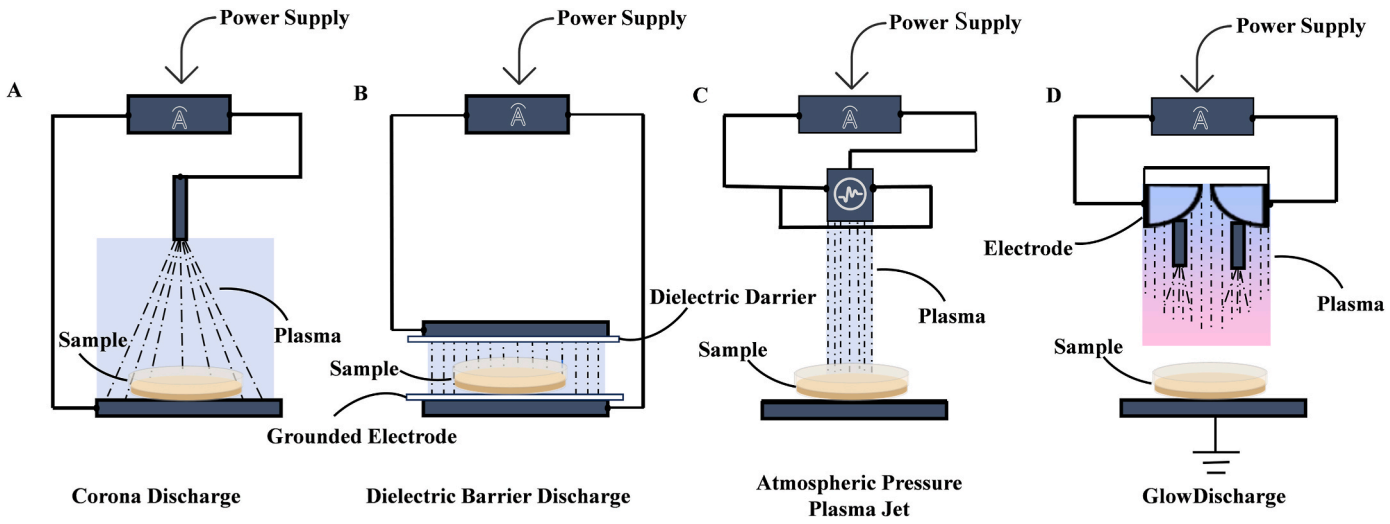

Fig. 1. Schematic illustration of discharge modes.

attributes were observed (Puligundla et al., 2018).

Among plasma-generation methods, DBD is one of the simplest and most widely used. In DBD systems, dielectric materials such as quartz or polymers are placed between two metal electrodes (Fig. 1B). Upon application of high voltage, the dielectric barrier suppresses arc formation and enables relatively uniform plasma generation across the discharge gap under ambient conditions, thereby providing stable and even treatment (Zhao et al., 2023b). Owing to its capability for homogeneous discharge with various working gases, DBD has become one of the most commonly applied discharge modes. DBD treatment at 45 V for 5 min achieved a maximum thiram reduction of 74% in tomato juice, and prolonged shelf life by decreasing pectin methyl esterase (PME) activity and total viable count from 23.1 to 11.2 mmol/min/g and from 5.6 to 1.4 log CFU/mL, respectively (Ali et al., 2024).

APPJ typically employ coaxial electrodes and a high-velocity gas flow (usually inert gases or gas mixtures) (Fig. 1C). A high-frequency, high-voltage electric field applied to the central electrode ionizes the flowing gas, generating reactive species that are transported through a nozzle and delivered to the target surface (Zhang et al., 2025). APPJs are relatively easy to operate; however, treatment outcomes can be sensitive to ambient conditions. Bakhshzadmahmoudi et al. (2022) found that treatment with an APPJ at a discharge power of 200 W for 6 min resulted in effective inactivation, reducing the bacterial count from 9.2×10^5 to less than 1.7 MPN/100 mL.

GD is generated when a direct-current voltage of ~100 V or higher is applied to a low-pressure gas (typically 1–1000 Pa), producing a stable glow between the cathode and anode (Fig. 1D). During electron capture at the anode, abundant positive ions (space charge) are formed between the electrodes; collisions between ions and electrons release photons, inducing gas excitation/ionization and sustaining the discharge (Laroque et al., 2022). GD can produce low-temperature plasma over a relatively large volume, although it requires more stringent operating conditions (Sakudo, Misawa, & Yagyu, 2020). Nitrogen AC glow discharge plasma, for example, markedly increased the intrinsic viscosity and gel-forming ability of pectin within 7 min at 0.1 Torr (Zheng et al., 2019).

Overall, among these systems, DBD and APPJ have been most extensively investigated due to their effectiveness in microbial inactivation and their ability to preserve food quality during processing.

2.3. Reactive species formation and activity

The reactive species in LTP are initiated by external energy sources, such as electric fields, microwaves, or laser radiation. These external energy inputs cause gas molecules to ionize, generating free electrons, ions, and excited molecules (Tappi et al., 2016). These excited species are highly reactive and can undergo processes such as electron capture, ionization, and dissociation, further producing free radicals and other reactive species (Kopuk et al., 2022).

2.3.1. Short-lived species

2.3.1.1. Hydroxyl radical. The hydroxyl radical (·OH) is an important intermediate in the formation of various other reactive species. The generation of ·OH is primarily associated with the dissociation of H_2O, and it is formed when plasma reacts with liquid, exhibiting high reactivity (Dharini et al., 2023). Its lifetime is on the order of 10^{-9} s, and it has an oxidation potential of 2.8 eV. Its lifetime is on the order of 10^{-9} s, and it has an oxidation potential of 2.8 eV (Phaniendra et al., 2015). Its main functions include hydrogen atom abstraction, electrophilic addition, and transfer (Dharini et al., 2023). It could non-selectively attack microbial membrane lipids, proteins, and DNA on a picosecond timescale, making it a primary factor in bacterial inactivation and the degradation of organic pollutants (Gligorovski et al., 2015; Joshi et al., 2011; Khan et al., 2023).

2.3.1.2. Singlet oxygen. Singlet oxygen ($^1O_2$) has a relatively long lifetime (on the microsecond scale) and can penetrate biological membranes, continuously oxidizing sensitive amino acid residues such as tryptophan and methionine, thereby enhancing the antimicrobial activity against resistant bacteria (Han et al., 2023; Tolouie et al., 2018). $^1O_2$ is an oxygen molecule in an excited state, with its primary source during plasma discharge being the combination of oxygen and electrons. In the gas phase, $^1O_2$ has a relatively long lifetime (75 min), while in the liquid phase, it has a shorter lifetime (2 μs) with an excitation energy of 1.0 eV. $^1O_2$ exhibits strong oxidative properties—stronger than superoxide anions, but weaker than hydroxyl radicals.

2.3.1.3. Superoxide anion. Superoxide anion (O_2^-) possesses relatively weak oxidative activity but can act as a "precursor," being converted into ·OH and $^1O_2$ via disproportionation or metal-catalyzed reactions, thereby amplifying oxidative chain processes (Teng et al., 2021). O_2^- exists as an excited-state oxygen species, with its primary formation during plasma discharge arising from the combination of oxygen and electrons (Teng et al., 2021). Moreover, O_2^- serves as a key source for $^1O_2$ generation, while hydrogen peroxide (H_2O_2) can also be transformed into $^1O_2$.

2.3.2. Long-lived species

2.3.2.1. Hydrogen peroxide. Hydrogen peroxide (H_2O_2) is relatively stable and strongly oxidative, allowing it to accumulate during plasma treatment (Han et al., 2023). Its molecular structure confers greater stability compared to other reactive oxygen species. H_2O_2 formation is primarily associated with ·OH and water molecules. In the liquid phase, it acts as a "reservoir," continuously releasing ·OH through homolytic or catalytic decomposition, thereby prolonging post-plasma oxidative effects and contributing to food preservation by inhibiting ethylene-induced ripening and delaying spoilage (Gao et al., 2023).

2.3.2.2. Ozone. Ozone (O_3) consist of three oxygen atoms, and their unpaired electrons, along with the arrangement of oxygen nuclei at the center, confer a high reactivity (Guzel-Seydim et al., 2004). O_3 formation involves two processes: the splitting and combining of oxygen molecules. The oxygen molecule splits at high energy into two free oxygen radicals, which later combine with oxygen either through heat or light to form an O_3 molecule (Niveditha et al., 2021). O_3 leaves no residues, as excessive O_3 rapidly decomposes to oxygen, typically within min (Pandiselvam et al., 2019). The inactivation mechanism of O_3 is through the progressive oxidation of cellular constituents. Its antimicrobial activity is primarily based on this oxidizing potential, which causes visible damage to fatty acids and proteins in the cellular components of pathogenic microbes (Niveditha et al., 2021). DBD plasma has become a primary method for O_3 production due to its advantages of operating at room temperature, having a simple structure, and being easily scalable. O_3 production can be achieved by applying high-voltage electric discharge in pure oxygen or ambient air.

2.3.2.3. NOx-derived acidification. Nitric oxide (NO) is a neutral reactive species that acts as an antioxidant due to its strong reducing ability (Dharini et al., 2023). NO can be generated through multiple pathways in plasma; among these, the reaction of atomic oxygen with molecular nitrogen is considered the most significant. Both NO and its derivative peroxynitrite ($ONOO^-$) exhibit dual nitrating and oxidizing activities, enabling disruption of bacterial cell membranes and induction of nucleic acid nitration damage (Pérez et al., 2022; Shen et al., 2019). Additionally, NO mediates plasma-induced acidification through the formation of HNO_2/HNO_3 (Ahmed et al., 2025); together with long-lived H_2O_2, these species enhance the liquid's germicidal activity and overall antimicrobial efficacy (Anderson, Cha, Lindsay, Clark, & Graves, 2016).

The presence of short-lived species (·OH, $^1O_2$, and $O_2^{\bullet-}$) has been evidenced using Electron paramagnetic resonance spin-trapping, optical diagnostics (OES/LIF), and chemical probe/scavenger assays, which are commonly employed to validate their formation in plasma systems (Cabrellon et al., 2020; Gorbanev et al., 2018; Misra et al., 2019; Zaplotnik et al., 2021).

Fluorescent probes offer several advantages, including high sensitivity, strong selectivity, capability for multi-component detection, and broad applicability (Wang et al., 2017). Fluorescent probes for ·OH are typically aromatic compounds. Among them, coumarin is recognized as a sensitive and selective probe for ·OH, as its reaction with hydroxyl radicals yields several hydroxylated products (Leandri et al., 2019).

Electron Paramagnetic Resonance (EPR) spectroscopy is a well-established technique capable of detecting unpaired electrons with high sensitivity (Steen et al., 2024). For example, 2,2,6,6-tetramethylpiperidine is commonly used as a trapping agent for $^1O_2$, reacting with it to form the stable nitroxide radical 2,2,6,6-tetramethyl-1-piperidinyloxy, which exhibits a characteristic EPR signal (AliaMohanty & Matysik, 2001).

In addition, a surface-enhanced Raman scattering-based sensing platform using gold nanoparticle/dopamine (AuNPs/DA) probes has been developed for superoxide anion detection. In this approach, dopamine is easily oxidized to dopamine quinone by superoxide anions, and the resulting AuNPs/dopamine-quinone complex exhibits characteristic Raman bands at 1270, 1335, and 1480 cm^{-1} at pH 10.0. Thus, the concentration of superoxide anions can be quantitatively determined by measuring the intensity of these SERS signals (Qin, Li, Kang, & Mu, 2015).

3. Mechanisms and applications of LTP for food safety control

The efficacy of LTP treatment primarily stems from the interactions between its diverse reactive species (e.g., •OH, O_3, $^1O_2$, NO•) and the target contaminants. For small-molecule organic pollutants (e.g., pesticides, mycotoxins), the primary mechanism involves chemical oxidative degradation. In contrast, for biological hazards (e.g., microorganisms, allergens), the effect is mainly achieved through the inactivation of their critical biological macromolecules.

3.1. Degradation of small-molecule organic contaminants

3.1.1. The potential mechanisms effectively remove pesticide residues

Plasma-driven pesticide transformation is dominated by RONS-mediated oxidation and radical reactions, often coupled with oxidative desulfuration (P=S→P=O), hydrolysis, key bond scission, and dealkylation/de-substitution processes. These reactions can further trigger hydroxylation and dehalogenation, aromatic ring opening, and deep oxidation, ultimately yielding low-molecular-weight organic acids and, in some cases, mineralization products **(**Table S2**).** However, pesticide degradation efficiency is matrix-dependent, and the observed differences are governed by the accessibility of reactive species to contaminated sites and mass-transfer limitations within the matrix. Using soybean seeds as an example, Anbarasan et al. (2022) reported that at an O_3 concentration of 550 mg L^{-1} and a treatment time of 6 min, the degradation of chlorpyrifos in high-loading samples (26%) was lower than that in low-loading samples (33%). This was attributed to a "shielding effect" caused by oxidized pesticide aggregates/product layers formed on the outer seed surface, which reduced O_3 diffusion and effective contact with the pesticide, thereby weakening the apparent oxidation efficiency. Similarly, under PAW washing conditions, Arcega et al. (2022) observed pesticide removals of 52–89% in fruit matrices, whereas the maximum reduction efficiencies of metribuzin and metobromuron in chrysanthemums were only 74% and 38%, respectively. This was mainly ascribed to the rough, layered-petal surface of chrysanthemums, which creates numerous inaccessible micro-sites and thus limits washing efficacy and reactive-species contact.

In addition, differences in pesticide chemical structures and functional groups can further amplify matrix effects, leading to pronounced variability in removal performance even within the same matrix. It has been suggested that pesticides with relatively fewer C–C bonds may be more readily degraded than those with more C–C bonds (Wang et al., 2019). Consistently, metribuzin, which contains fewer C–C bonds than metobromuron, was removed more efficiently from chrysanthemums: the minimum residues decreased to 40.1 and 56.7 μg/kg, corresponding to maximum reduction efficiencies of 74% and 38%, respectively (Arcega et al., 2022). In corn, air plasma treatment (1000 mL min^{-1}, 20 W, 1200 Hz, 60 s) reduced chlorpyrifos and carbaryl residues by up to 86% and 67%, respectively (Liu et al., 2021). The lower removal of carbaryl was attributed to its structural recalcitrance; its naphthalenol moiety is more stable than the nitrogen-containing heteroaromatic ring in chlorpyrifos, making chlorpyrifos more susceptible to attack by plasma-generated radicals and high-energy electrons and thus more readily eliminated.

LTP-induced pesticide degradation is primarily attributed to multiple mechanisms involving RONS, electric fields, and ultraviolet radiation. RONS, as strong oxidizing agents with high oxidation-reduction potentials, can directly attack pesticide molecules or indirectly initiate chain reactions to break their key chemical bonds. In the LTP treatment of thiram, OH and H_2O_2 radicals are the key reactive species responsible

for degradation, with the reduction process involving hydrolysis and oxidative cleavage of C=S, S-S, and C-N bonds, generating various intermediate products, including dimer II and carbon disulfide (Fig. 2A) (Murtaza, Liao, et al., 2024).

Ozone, as a stable oxidant produced during plasma discharge, plays a crucial role in pesticide degradation, particularly through its efficient oxidative properties in the aqueous phase, known as aqueous ozonation. O_3 molecules can attack unsaturated aliphatic structures and undergo oxidative cleavage, significantly altering the molecular structure of pesticides. The oxygen plasma degradation of dichlorvos follows two parallel or independent pathways: It was possible that dichlorvos was degraded during oxygen plasma treatment via two pathways (Fig. 2B). First route is based on free radical reaction initiated by free radical generated in plasma. Another pathway may be suggested by addition reaction in which the electrons provide energy and impact the reaction involved in unsaturated bonds within dichlorvos molecule. Possibly, both stages take place nearly simultaneously. Concretely speaking, if a dichlorvos molecule is exposed to oxygen plasma (Bai et al., 2010).

Additionally, ultraviolet radiation associated with plasma has been proven to be an effective means of pesticide degradation. LTP removes chlorpyrifos through UV-induced degradation and surface etching. In UV-assisted degradation, the removal of ethyl group and chloro group will start the degradation (initiated with ethyl group removal and then chloro group removal or wise versa) to form O-ethyl-O-(3,5-dichloro-2-pyridil)-hydrogene-phosphorothioate (Fig. 2C). Further sequential removal of chloro and ethyl group results in the formation of O-(5-chloro-2-pyridil)-dihydrogene-phosphorothioate (Anbarasan et al., 2022).

The degradation mechanisms of LTP and PAW treatments show minimal differences, which can be attributed to the dominant role of hydrolysis in the PAW process. The degradation of chlorpyrifos and chlorpyrifos oxone derivatives follows a typical two-stage pathway (Fig. 3A): first, hydroxyl radicals oxidize the P=S bond to a P=O bond, and then hydrolysis becomes the dominant process, leading to the cleavage of P–O and O–P bonds to form 2-isopropyl-6-methyl-4-pyridinol and diethyl phosphate. Primary products such as 3,5,6-trichloropyridinol can further be transformed into polyol derivatives through substitution reactions, eventually undergoing oxidation to form diketones and other compounds (Khan et al., 2021).

It is noteworthy that although LTP can decompose pesticides into low-toxicity small molecules or ultimately mineralize them, some transformation products with higher toxicity than the parent pesticide may be generated during the process. Dimethoate can oxidize to its more toxic oxo-analogue, omethoate. In the degradation pathway of chlorpyrifos, intermediate products such as P2 and P5 still maintain significant toxicity (Fig. 3B) (Xu et al., 2023). Therefore, when assessing the safety of LTP technology, it is essential to strengthen the identification and toxicity evaluation of transformation products to ensure that its application does not introduce new environmental risks.

3.1.2. *Mechanisms of mycotoxin degradation by LTP*

3.1.2.1. Oxidation reactions. AFB1, the most potent toxin within the aflatoxin group, poses mutagenic, teratogenic, and carcinogenic risks to humans. Low-moisture commodities like nuts, peanuts, corn, wheat, and rice are frequently prone to aflatoxin contamination (Rao et al., 2023). The toxicity of aflatoxins (AFTs) primarily stems from the C8=C9 double bond in the furofuran ring (Liu et al., 2021; Neuenfeldt et al., 2023). The degradation of AFB1 results in reduced bioactivity, which is attributed to the loss of this pivotal double bond, along with modifications to key

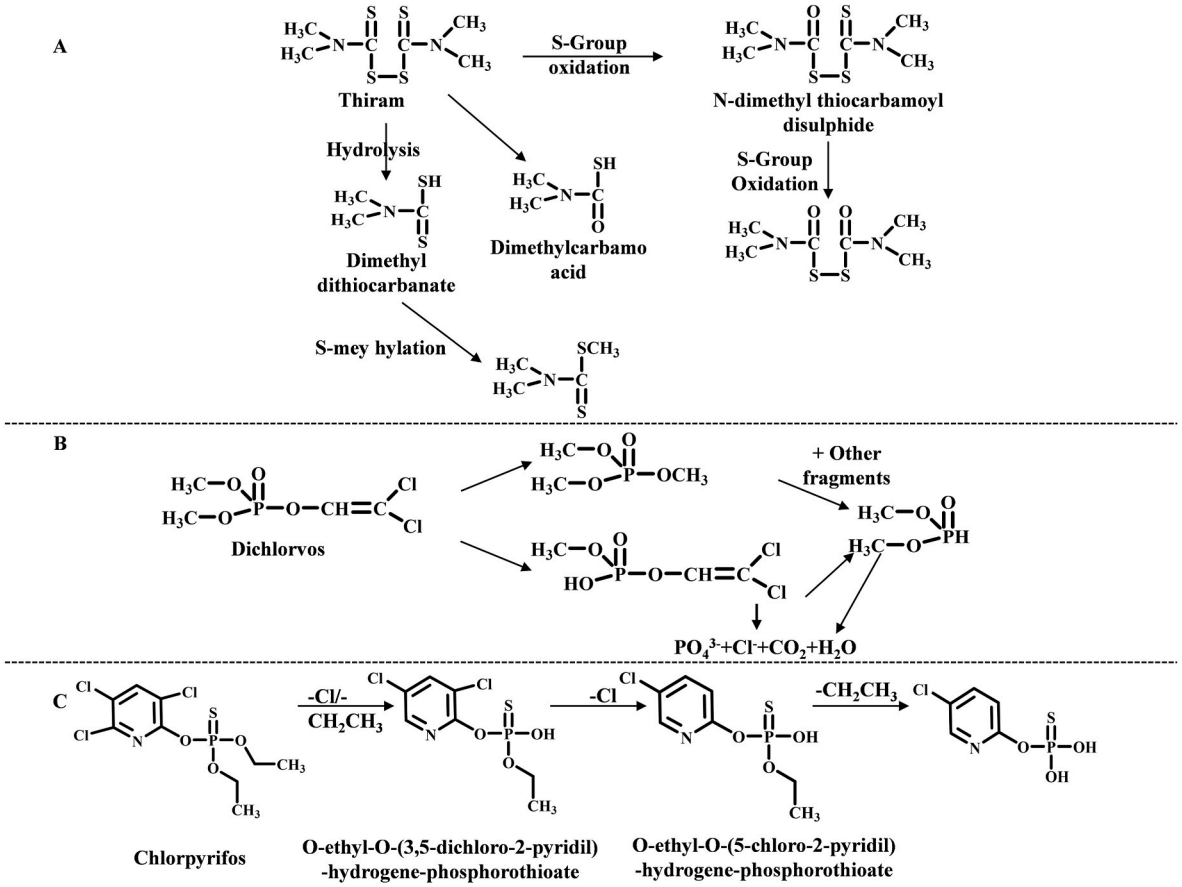

Fig. 2. Degradation pathway of various pesticides by plasma-based technologies. Degradation pathways of thiram by DBD plasma treatment (A); Dichlorvos degradation pathways under oxygen plasma treatment (B); Chlorpyrifos degradation pathways via cold plasma(C).

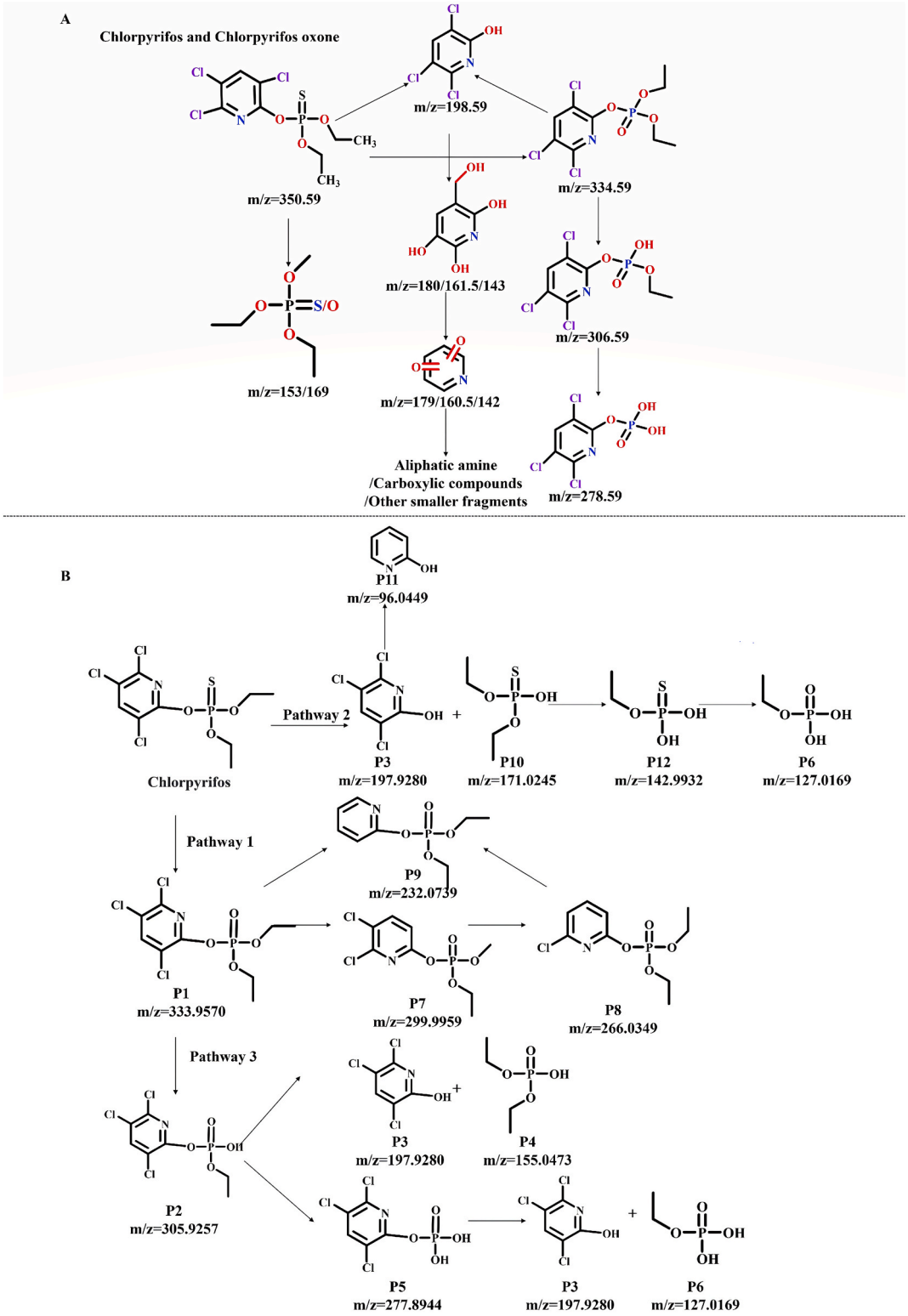

Fig. 3. Degradation pathway of various pesticides by plasma-based technologies. Chlorpyrifos, chlorpyrifos oxone degradation pathways via microplasma (A); chlorpyrifos degradation pathways via DBD plasma (B).

structures such as the lactone ring, cyclopentanone, and the methoxyl group (Wu et al., 2021). Shi et al. (2017) reported that under conditions of 40.0% relative humidity, a 5-min treatment with LTP resulted in a degradation rate of 76% for AFB1. The degradation pathway primarily involves epoxidation and oxidation reactions (Fig. 4A). On one hand, the concentration of hydrogen H_2O_2 generated by LTP increases with elevated humidity, which can attack the terminal double bond of AFB1, leading to epoxidation and the formation of the product AFB1-P1 ($C_{17}H_{13}O_7$, m/z 329.06). On the other hand, various oxygen-containing reactive species in the system, such as ·OH, H_2O_2, and O_3, collectively act on the furan ring of AFB1, triggering a ring-opening reaction that produces AFB1-P2 ($C_{14}H_{11}O_5$, m/z 261.07).

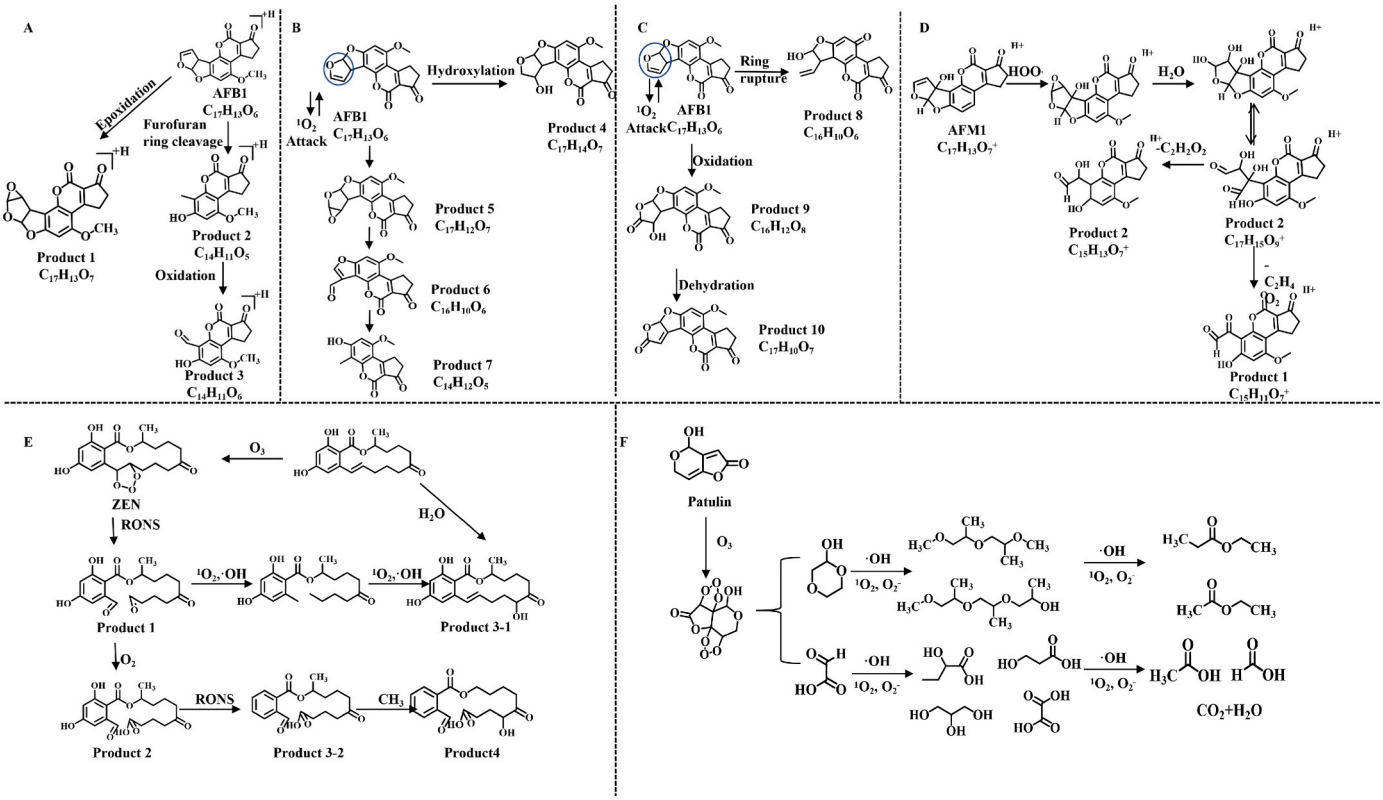

Fig. 4. Degradation pathway of various mycotoxins by plasma-based technologies. Oxidative degradation of AFB1 by high-voltage atmospheric cold plasma (HVACP) treatment (A); AFB1 degradation pathways under cold atmospheric plasma (CAP) treatment (B); AFB1 degradation pathways via plasma-activated water (PAW) (C); AFM1 degradation pathways (D); ZEN degradation pathways (E); Patulin degradation pathways (F).

This product is further oxidized to form AFB1-P3 ($C_{14}H_{11}O_6$, m/z 275.05). Under 40% moderate humidity, the degradation of AFB1 is likely the result of the synergistic action of multiple reactive species, including H_2O_2, •OH, H_2O_2, and O_3 (Fig. 4B).

Xu et al. (2023) further investigated the mechanisms during LTP treatment, hydroxyl radicals (•OH) serve as the primary reactive species, initiating hydroxylation at the furan ring to form AFB1-P4 ($C_{17}H_{14}O_7$, m/z 331.08). Subsequent attacks by ROS target the double bond of the furan ring, leading to AFB1-P5 ($C_{17}H_{12}O_7$, m/z 329.07). The unstable epoxide adduct of P2 then readily decomposes to AFB1-P6 ($C_{16}H_{10}O_6$, m/z 299.06) (Shi et al., 2017; Xu et al., 2023), with final ring cleavage yielding AFB1-P7 ($C_{14}H_{12}O_5$, m/z 261.07). In contrast, PAW treatment predominantly involves $^1O_2$, which triggers epoxidation, demethylation, and oxidation. This process first disrupts the methyl group on the benzene moiety, generating AFB1-P8 ($C_{16}H_{10}O_6$, m/z 299.05) (Hojnik et al., 2021). Oxidation of the terminal furan ring's double bond follows (Fig. 4C), forming AFB1-P9 ($C_{17}H_{12}O_8$, m/z 345.06) (Zhang, Sun, et al., 2022), which subsequently undergoes dehydration to produce AFB1-P10 ($C_{17}H_{10}O_7$, m/z 327.05) (Zhang, Sun, et al., 2022).

Aflatoxin M1 (AFM1) is the principal hydroxylated metabolite of AFB1 and is produced through the action of CYP1A2 (Nikmaram & Keener, 2022). The degradation of AFM1 primarily occurs via a hydration reaction at the C_8=C_9 double bond of its furan ring, which is highly susceptible to attack by LTP-generated ROS, such as hydroxyl radicals and hydrogen peroxide, among others (Wu et al., 2021). This reaction yields a dihydroxylated product, AFM1-P2 ($C_{17}H_{15}O_9$, m/z 363.0711). AFM1-P2 can further decompose into secondary degradation products, AFM1-P1 and AFM1-P3, through the release of glycolaldehyde and the cleavage of glyoxylic acid, respectively (Fig. 4D) (Nikmaram et al., 2023).

ZEN is a non-steroidal estrogenic mycotoxin produced by *Fusarium* (Chang et al., 2017). Its structure, similar to naturally occurring estrogens, allows it to competitively bind to mammalian estrogen receptors, leading to sterility and reproductive disorders in animals (Shier et al., 2001). Liu et al. (2025) observed after treatment with LTP at 30W for 3 min, the degradation rate of ZEN reached 96%. In the LTP treatment, ROS/RNS attack the olefinic double bond of ZEN, causing bond cleavage and the formation of aldehyde groups at both ends, resulting in the product ZEN-P1. ZEN-P1 undergoes further oxidation by ROS/RNS, with the aldehyde group farthest from the benzene ring being oxidized to a carboxyl group, forming ZEN-P2. Subsequently, under the electrophilic action of ROS/RNS, the OH-1 and OH-3 groups on the benzene ring of ZEN-P2 are disrupted, converting it to ZEN-P3-2. This product ultimately undergoes demethylation, resulting in the formation of ZEN-P4 (Fig. 4E).

Patulin is a neurotoxic secondary metabolite produced by *Aspergillus*, *Byssochlamys*, and *Penicillium*, which causes severe toxicity in animal tissues (Moake et al., 2005). Reactive species such as O_3 and ·OH initially attack the conjugated double bonds of patulin via cycloaddition reactions, disrupting its lactone ring structure and generating intermediates such as 1,4-dioxane-2-ol and glyoxylic acid. Subsequently, 1,4-dioxane-2-ol undergoes ring-opening and further oxidation to form products including monomethyl propylene glycol, 1-(2-methoxy-1-methylethoxy)-2-propanol (Sajid et al., 2018), which are further converted into ethyl acetate and ethyl propionate. Meanwhile, the oxidation pathway of glyoxylic acid produces various small organic acids and alcohols (El Hajj Assaf et al., 2019). These short-chain acids, alcohols, and ethers are ultimately oxidized to acetic acid, formic acid, CO_2, and H_2O, achieving complete mineralization of patulin (Fig. 4F) (Xue et al., 2021).

3.1.2.2. Bond cleavage. OTA is commonly found in dried fruits such as raisins, is recognized as one of the most hazardous mycotoxins

(Covarelli et al., 2012). The IARC has classified OTA as a Group 2B carcinogen, posing significant health risks to the human kidneys, nervous system, and immune system (Abrunhosa et al., 2016). Under 21 kV gas-phase surface discharge plasma treatment, more than 62% of OTA was degraded within 4 min, with complete degradation achieved after 10 min (Wang et al., 2024). During this degradation process, OTA initially undergoes decarboxylation to form OTA-P1. OTA-P2 and OTA-P4 are produced through the hydrolysis of OTA. OTA-P2 then undergoes a dehydration reaction to generate OTA-P3, which may subsequently undergo dehydrogenation to form product OTA-P5 (Fig. 5A) (Wang et al., 2024).

DON is a type B trichothecene mycotoxin produced by *Fusarium*. Inappetence and vomiting are common symptoms of exposure to DON (Zhuang et al., 2020). It also exhibits hepatotoxicity, nephrotoxicity, immunotoxicity, genetic toxicity, and neurotoxicity (Yan et al., 2020). The hydroxyl group at the C_3 position and the unsaturated bond between C_9 and C_{10} are key structural features contributing to the toxicity of DON. DON undergoes degradation through hydroxylation, de-epoxidation, oxidation, and substitution reactions (Fig. 5B). Water molecules can add to the C9=C10 double bond or the epoxide group, producing the hydroxylated product DON-P1 ($C_{15}H_{22}O_7$). De-epoxidation of the epoxide at C12–C13 generates DON-P2, known as de-epoxy deoxynivalenol (DOM-1, $C_{15}H_{20}O_5$), which exhibits significantly lower toxicity than DON. DOM-1 can be further degraded: cleavage at the unstable C12 position, dehydration of the C3 hydroxyl to form a double bond, and oxidation of the C7 hydroxyl to a ketone ultimately yield DON-P3 ($C_{14}H_{16}O_4$). Additionally, substitution of the C3 hydroxyl with a nitro group, oxidation at C7, and hydration of the C9=C10 double bond or epoxide ring collectively produce the nitrogen-containing derivative DON-P4 ($C_{15}H_{21}NO_9$) (Chen et al., 2022).

3.1.3. Functional group modification

3.1.3.1. AFB1 hydration. In the LTP system, H and •OH generated from the decomposition of water molecules are key reactive species that initiate AFB1 degradation, primarily through addition reactions (Fig. 5C). First, hydration reacts with the C8=C9 double bond of the furan ring in AFB1, leading to the formation of the product AFB1-P11 ($C_{17}H_{15}O_7$, m/z 331.08). Subsequently, the methoxy group of AFB1 undergoes cleavage, forming the intermediate AFB1-P12 ($C_{16}H_{13}O_6$, m/z 301.07). This intermediate's carbonyl group is further hydrogenated, converting it into the degradation product AFB1-P13 ($C_{16}H_{17}O_6$, m/z 305.10). Another reaction pathway involves the addition of an aldehyde group (CHO) to AFB1, resulting in the intermediate AFB1-P14 ($C_{19}H_{15}O_8$, m/z 371.08). The lactone ring in the molecule of AFB1-P14, along with the cyclopentanone site, undergoes further hydrogenation, ultimately generating AFB1-P15 ($C_{19}H_{19}O_8$, m/z 375.10) (Shi et al., 2017).

MC-LR, a toxic pollutant from *Microcystis aeruginosa*, is frequently found in eutrophic waters worldwide and is included in water quality risk management frameworks (Wynne et al., 2010). It causes bioaccumulation and toxic effects in top predators, including humans, through direct exposure and trophic transfer. The Adda group in MC-LR is highly reactive, particularly with hydroxyl radicals, with the conjugated double bond, benzene ring, and methoxy group being vulnerable to attack (Liang et al., 2021; Zhang et al., 2012). The diene bonds on the Adda chain are closely linked to MC-LR toxicity, with their cleavage being a key factor in reducing toxicity (Liang et al., 2021).

Under LTP treatment, MC-LR degradation follows a sequential hydroxyl radical-mediated oxidation and bond cleavage process (Fig. 6). Initial hydroxylation of the Adda group's conjugated double bond forms MC-LR-P1 (m/z 1029.50). Further hydroxylation of the benzene ring and double bond yields MC-LR-P2 (m/z 1045.00), and additional hydroxylation leads to MC-LR-P3 (m/z 1027.50) and MC-LR-P4 (m/z 1011.50). Cleavage of the C6–C7 bond forms MC-LR-P5 (m/z 835.30), while oxidation of remaining structures creates MC-LR-P6 (m/z 829.30). Further cleavage at C4–C5 produces MC-LR-P7 (m/z 815.40), which undergoes further oxidative degradation, eventually converging into the low-molecular-weight product MC-LR-P9 (m/z 642.10) (Wang et al., 2024).

3.1.4. Biological inhibition pathways

LPS is one of the primary components of the cell walls of Gram-negative bacteria and certain cyanobacteria (Huang et al., 2011). It is released during cell proliferation, death, and lysis, making it prevalent

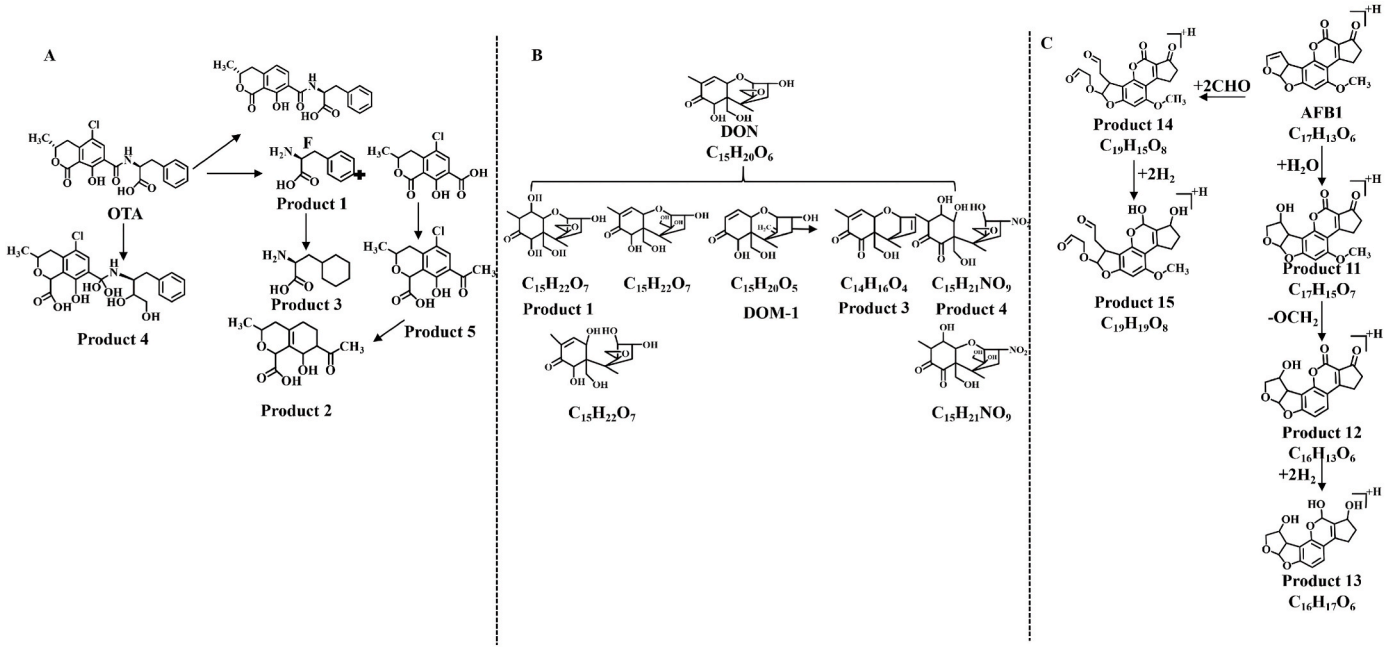

Fig. 5. Degradation pathway of various mycotoxins by plasma-based technologies. Ochratoxin A degradation pathways(A); Deoxynivalenol degradation pathways (B); AFB1 degradation pathways (C).

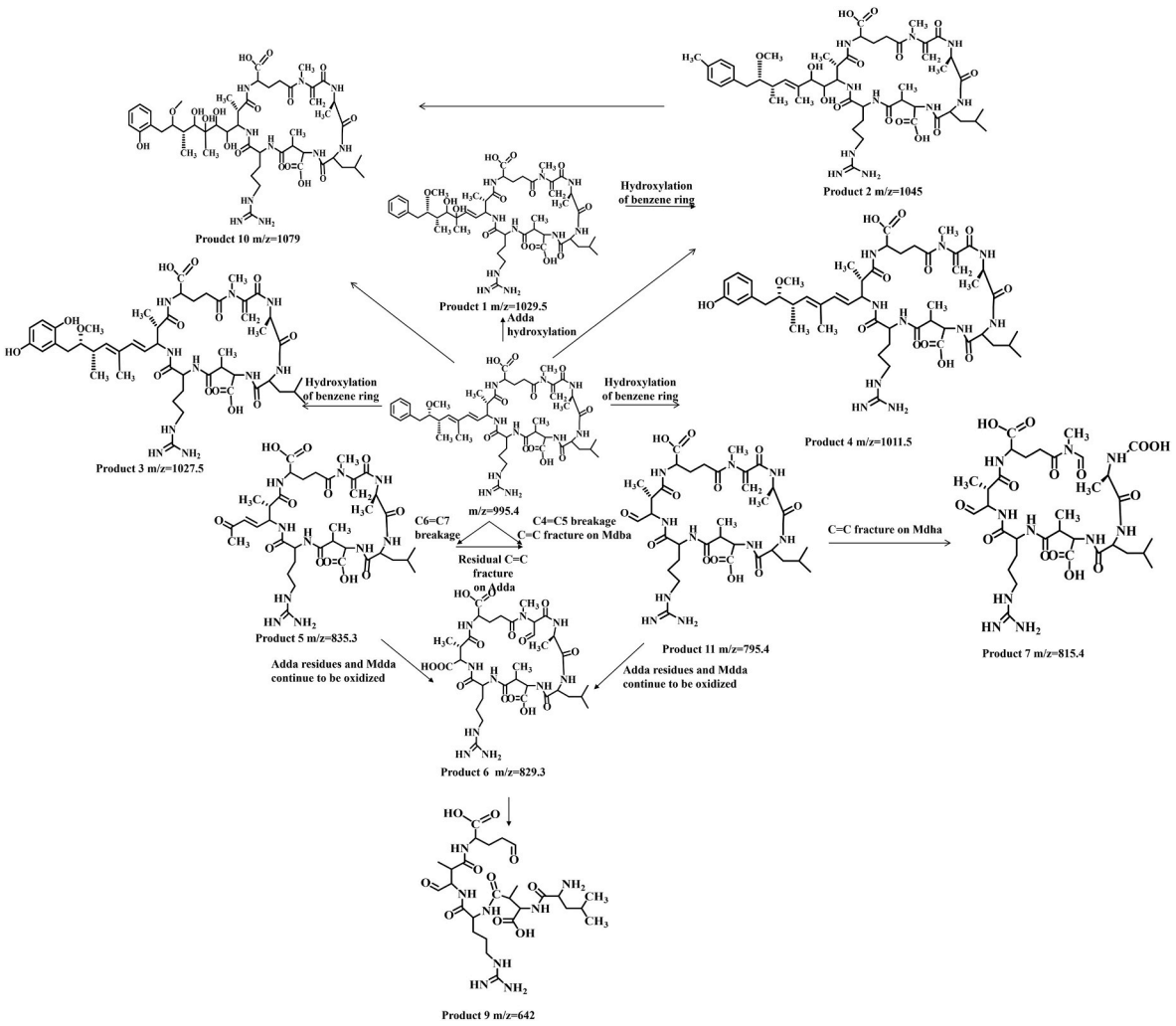

Fig. 6. Degradation pathway of Microcystin-LR degradation pathways by plasma-based technologies.

in wastewater treatment plants and tailwater (Xue et al., 2019). Bacterial endotoxins in reclaimed water are a significant factor that can lead to lung inflammation. LTP effectively inhibits endotoxin synthesis by downregulating key genes in the biosynthetic pathway (*KO00540*), such as K06041 (*KdsD*), K00677 (*LpxA*), and K02536 (*LpxD*) (Zhang, Wang, et al., 2022). Since endotoxin synthesis depends on the structural integrity of the Gram-negative bacterial cell wall, LTP further disrupts this process by suppressing peptidoglycan-related gene expression, thereby impairing cell wall formation and reducing endotoxin production (Zhang, Sun, et al., 2022). LTP technology primarily inactivates endotoxins through active species generated during treatment with lipid peroxidation. Hydroxyl radicals extract hydrogen atoms from polyunsaturated fatty acids in the lipid A component of endotoxins, forming lipid radicals. These radicals react with molecular oxygen to produce lipid peroxides, which further propagate the chain reaction by removing hydrogen from nearby fatty acids, forming lipid hydroperoxides and new lipid radicals. Once initiated, this lipid peroxidation cascade continues, ultimately impairing the biological activity of endotoxins by damaging lipid A, the core functional site.

3.1.4.1. Gene-expression suppression. Fungal toxin production may be suppressed by interfering with the expression of genes involved in the biosynthetic pathway. Aflatoxin biosynthesis occurs via a polyketide pathway governed by more than 25 genes. The majority of these genes, including *aflA, aflC, aflD, aflE, aflG, aflJ, aflM, aflP, aflQ, aflR,* and *aflS*, are predominantly involved in the biosynthesis of AFB1. Among them, *aflR* and *aflS*, as regulatory genes, are pivotal in the aflatoxin bio (Hu et al., 2017) synthesis process. LTP can effectively reduce AFB1 production by inhibiting the expression of critical genes—namely, *aflC, aflE, aflM, aflR,* and *aflS*, that are integral to the aflatoxin biosynthesis pathway (Zhao et al., 2025).

3.2. Inactivation of biological hazards

3.2.1. The potential mechanisms for effective microbial inactivation

LTP contains abundant high-energy particles, reactive radicals, and UV photons, and is characterized by a low apparent temperature, residue-free operation, and relatively low cost, making it promising for microbial decontamination of food products. To date, LTP has been demonstrated to effectively control common foodborne pathogens in foods, including Gram-negative bacteria (e.g., *E.coli*), Gram-positive bacteria (e.g., *Listeria monocytogenes*), and fungi (Table S3). Their distinct cell-envelope architectures may partly account for differences in plasma susceptibility: Gram-negative bacteria possess an outer membrane rich in LPS and a thin peptidoglycan layer (~2 nm), whereas Gram-positive bacteria have a thicker and more rigid peptidoglycan layer (~40 nm). Under identical LTP conditions (1 atm, 58 kHz, 20 kV, air) on pork, the Gram-negative *E. coli* exhibited a greater reduction (~1.5 log) than the Gram-positive *L. monocytogenes* (~1.0 log) (Choi et al., 2016), consistent with the commonly reported higher plasma sensitivity of Gram-negative bacteria relative to Gram-positive bacteria. In contrast, fungi often show higher tolerance to LTP, likely because

their cell walls are primarily composed of chitin, which is generally more rigid than bacterial peptidoglycan. Under identical LTP conditions (20 kPa, Ar, 1.2 kV, 20–100 kHz, 10 min) on pork, yeasts and molds exhibited a smaller reduction (0.4 log) than psychrotrophs (1.2 log) (Ulbin-Figlewicz et al., 2015), indicating greater plasma resistance of fungal populations. Moreover, LTP can also inactivate certain highly resistant spores. Zhao et al., 2023a reported that LTP achieved a 4.0-log inactivation of *Alicyclobacillus acidoterrestris* spores in apple juice. The LTP generation process involves ultraviolet radiation, charged particles, strong electric fields, metastable particles, free radicals, and other highly reactive species. These physicochemical factors, through the generation of high-energy particles and strong electric fields, directly affect bacterial structures, damaging their cell walls and membranes, and impairing normal cellular functions. The ultraviolet radiation, accumulation of charged particles, electroporation induced by strong electric fields, and oxidative stress from ROS and RNS generated by LTP lead to the destruction of bacterial cell walls, membranes, nucleic acids, and proteins, thereby inhibiting growth and inducing cell death. LTP inactivation mechanisms are diverse and complex, involving physical, chemical, and biological processes (Fig. 7),which are discussed in detail in subsequent sections.

3.2.1.1. Cell wall and membrane damage. Distinct cell-envelope architectures may partly account for the different plasma susceptibilities among microorganisms. Compared with Gram-positive bacteria, Gram-negative bacteria are generally more sensitive to LTP, largely because their outer membrane contains lipopolysaccharide (Daş et al., 2006; Laroussi et al., 2003). Reactive oxygen species such as •OH, HO_2•, and O_3 can oxidatively modify and structurally disrupt LPS by attacking C–O, C–C, C–N, and C–H bonds, abstracting hydrogen atoms and promoting the formation of conjugated C=O and C=C structures (Yusupov et al., 2015). This process compromises the barrier function of the outer membrane and facilitates subsequent oxidative damage (e.g., lipid peroxidation), ultimately impairing membrane integrity. In contrast, the Gram-positive cells have stable and thicker peptidoglycan layers (around 40 nm), which may partially buffer plasma attack; therefore, lethality is often associated with oxidative injury to intracellular biomacromolecules (e.g., proteins and nucleic acids) in addition to envelope perturbation.

Wang et al. (2022) investigated LTP against Fusarium spp. and reported that spore surfaces were relatively smooth before treatment, whereas LTP exposure caused discernible surface destruction, accompanied by damage to the spore cell wall and membrane and leakage of intracellular constituents. Compared with bacteria, fungi may be more resistant to plasma-generated reactive species because their cell walls contain chitin, which is mechanically more rigid than bacterial peptidoglycan (Wang et al., 2022). Notably, existing studies more frequently report damage to the fungal cell wall or the outer layers of spores, and such wall-associated injury is often considered a critical determinant of fungal inactivation. These changes are commonly attributed to RONS-driven oxidation of the cell wall and plasma membrane, which increases wall permeability and triggers secondary membrane destabilization (e.g., lipid peroxidation and membrane-potential disruption), and may further promote pore formation via electroporation, thereby accelerating leakage and inactivation (Gan et al., 2021; Ravash, Hesari, Feizollahi, & et al, 2024). In addition, ergosterol, the major sterol in the fungal cytoplasmic membrane, is essential for maintaining membrane integrity; cold plasma has been reported to decrease ergosterol levels, thereby inhibiting fungal growth and proliferation (e.g., *Alternaria alternata*) (Du et al., 2023; Kong et al., 2019).

3.2.1.2. Electroporation and electrostatic disruption. The cell membranes (cytoplasmic membrane and outer membrane) are vulnerable to physical disruption by LTP (Montie et al., 2000). *Vibrio parahaemolyticus* cells

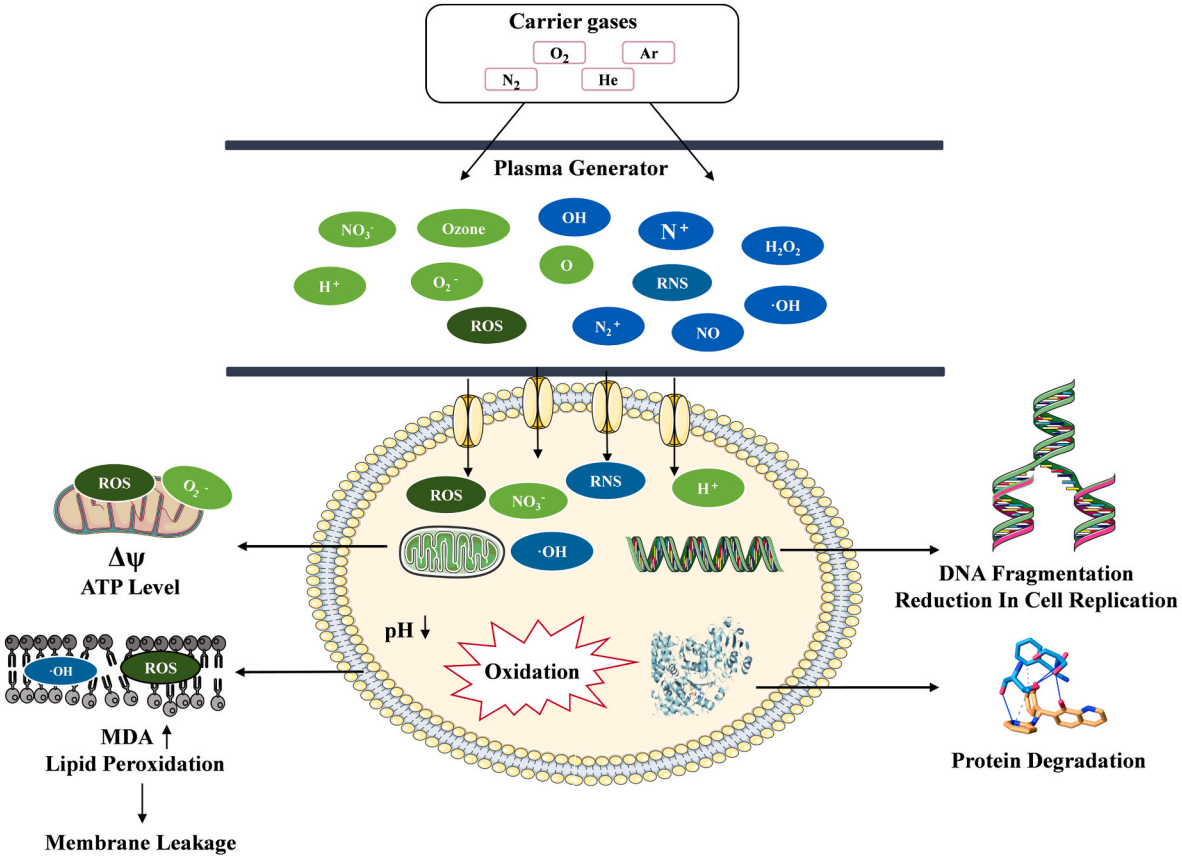

Fig. 7. Mechanisms of microbial inactivation by LTP.

exposed to LTP transform from intact rod-shaped forms into shriveled, irregular structures, accompanied by substantial nucleic acid and protein leakage, indicating severe membrane damage (Zhang et al., 2024). Electroporation is considered a dynamic phenomenon that depends on the local transmembrane voltage at each point on the cell membrane. For a given pulse duration and waveform, a specific transmembrane voltage threshold is generally required to initiate electroporation. When the outer membrane accumulates sufficient electrostatic charge such that the resulting outward electrostatic stress exceeds its tensile strength, cell lysis may occur (Z. Yang and Liu, 2021). Moreover, electroporation creates nanopores in the membrane, and the subsequent expansion of these pores can lead to irreversible damage, allowing intracellular contents to leak out and triggering apoptosis. If the electric field intensity reaches or exceeds a second threshold, irreversible electroporation occurs, compromising cell viability.

The destructive effects of LTP are also closely associated with ROS/RNS, which alter membrane and cell wall structures and promote the release of cytoplasmic contents (Hati, Patel, & Yadav, 2018). Compared with Gram-positive bacteria, Gram-negative bacteria are more sensitive to LTP treatment, primarily due to the presence of LPS, a key component of their outer membrane (Dong et al., 2017). LPS exhibits a higher charge density per unit surface area than any phospholipid, facilitating charge accumulation and thereby enhancing the susceptibility of these bacteria to electric fields. Furthermore, electric fields can reorient membrane proteins, leading to their denaturation and functional loss, a direct consequence of electrostatic perturbations to the outer membrane (Huang et al., 2013).

3.2.1.3. Particle bombardment and etching. During LTP discharge, energetic electrons collide with gas molecules, triggering ionization, excitation, and dissociation, thereby generating charged species (electrons/ions) as well as a broad spectrum of RONS. Under typical LTP conditions used for food processing, charged species more often contribute via surface deposition/charging rather than high-energy bombardment: charge accumulation on microbial surfaces can induce localized electric fields and electrostatic stresses, leading to roughening and micro-defect formation in the cell envelope (cell wall/outer membrane and cytoplasmic membrane) and increasing permeability, which facilitates subsequent RONS penetration and oxidative attack (Zhang et al., 2023). Devi et al. (2017) observed pronounced rupture of the outer layers of peanut-associated fungal spores after LTP treatment by electron microscopy and attributed this to surface charge build-up and sustained erosion of the outer layer by reactive plasma species.

However, other studies have suggested that ion bombardment contributes only marginally to microbial inactivation under atmospheric-pressure conditions. Because collisions are frequent at 1 atm, positive ions typically reach the sample surface with low mean kinetic energies (<1 eV), and electron number densities are often several orders of magnitude lower than the flux of neutral reactive species (Choi et al., 2007; Kim et al., 2006; Soria, Pontiga, & Castellanos, 2004; Stafford & Kushner, 2004). Therefore, the dominant contribution is more likely the synergistic interplay between localized electric-field/electrostatic-stress effects induced by surface charging (sometimes discussed in the context of ion-impact-related phenomena) and RONS-driven chemical etching/oxidative damage.

3.2.1.4. Lipid peroxidation. LTP-generated reactive species, including •OH, H_2O_2 and O_3, preferentially attack membrane phospholipids, particularly the polyunsaturated fatty acids (PUFAs) located near the membrane surface. During lipid-peroxidation chain reactions, ROS abstract hydrogen atoms from PUFAs, forming lipid radicals (L•) that subsequently react with molecular oxygen to yield lipid hydroperoxides (LOOH). LOOH further decomposes into malondialdehyde (MDA), which serves as a key marker of lipid oxidation (Guéraud et al., 2015). After 45 min of LTP activation, the MDA concentration in the bacterial suspension increased by 48%. The study by Heo et al. (2021) further confirmed this, showing that O_3 generated by DBD plasma induces lipid oxidation, producing MDA and increasing the thiobarbituric acid reactive substances (TBARS) value. The accumulation of MDA within microbial cells can damage DNA, ultimately leading to cell death (Thirumdas et al., 2015). The chain reactions following as L• → LOOH → MDA + secondary products. Resulting acyl-chain shortening alters membrane fluidity, causing structural rupture and osmotic imbalance (Abramzon et al., 2006). Synergistically, C-O and C-N bonds are broken and the bacterial cell loses the protection as the entire cell structure is damaged (Du et al., 2023). These processes disrupt membrane integrity and promotes leakage of intracellular constituents, providing additional entry routes for ROS and RNS. O_3 may also increase cell permeability and promote water loss by oxidizing membrane lipids (Pandiselvam et al., 2022). Once inside, these reactive species attack intracellular macromolecules, including polysaccharides, lipids, proteins, and DNA, initiating further oxidation, impairing essential cellular functions, and ultimately inactivating the microbe (Ravash, Hesari, Feizollahi, & et al, 2024).

3.2.1.5. Biomacromolecule damage

3.2.1.5.1. Nucleic acids. LTP causes strand breaks, base modifications, and DNA/RNA cross-linking, impeding replication/transcription. Agarose electrophoresis confirms progressive DNA fragmentation post-treatment. The bands became increasingly faint with longer exposure, indicating DNA loss and suggesting that LTP-generated ROS/RNS cleave DNA strands to produce fragments (Wang, Xing, et al., 2023). LTP produce highly energetic photons in the vacuum ultraviolet (VUV, 10-200 nm) and ultraviolet (UV, 100–400 nm) wavelength ranges (Golda et al., 2020). UV irradiation, particularly at 260 nm, is strongly absorbed by DNA, inducing the formation of pyrimidine dimers and strand breaks that disrupt DNA replication and transcription, compromise genomic integrity, and ultimately lead to cell death (Ekezie et al., 2017).

3.2.1.5.2. Protein inactivation. LTP-derived reactive species can compromise microbial viability by perturbing protein structure and function, thereby disrupting metabolic homeostasis. The major protein-targeted pathways include: (i) oxidative modifications—ROS oxidize free amino acids and proteins, promoting hydroxylation/oxidation of aromatic side chains, oxidation of –SH, and methionine sulfoxidation, which destabilize protein folding and impair the integrity of active sites; (ii) RNS-related nitration and S-nitrosylation—RNS can nitrate residues such as tyrosine and induce cysteine-associated S-nitrosylation, altering protein charge and conformation and suppressing enzymatic catalytic activity (Dharini et al., 2023); (iii) backbone disruption and cross-linking/aggregation—sustained oxidative stress may cause peptide-chain cleavage while also promoting protein crosslinking and aggregation, markedly reshaping secondary/tertiary structures and reducing solubility, ultimately inactivating key enzymatic systems and collapsing cellular physiology; and (iv) synergistic environmental factors—LTP-derived reactive species can lower pH, and acidification further affects enzyme activity and protein stability (Daş et al., 2006; Hertwig et al., 2015). In addition, $^1O_2$ has been implicated in surface "etching/oxidation" processes and in promoting protein oxidation (Davies, 2003), while the strong $ONOO^-$ can likewise drive protein modifications and accelerate functional loss. Han et al. (2019) reported that $\cdot OH/H_2O_2$ generated by APPJ oxidized the heme prosthetic group of HRP, resulting in enzyme inactivation, indicating that plasma-associated RONS can directly damage essential cofactors/active centers. Similarly, Guo et al. (2021) showed that PAW oxidatively damaged the receptor-binding domain of the SARS-CoV-2 spike protein and weakened its interaction with ACE2. Overall, non-specific oxidation can synergistically inactivate both structural and functional proteins, thereby promoting microbial inactivation.

3.2.1.6. Metabolic and homeostasis imbalance

3.2.1.6.1. Energy metabolism disorder. Mitochondrial dysfunction is closely associated with plasma-induced microbial inactivation. Reactive species generated during LTP treatment may penetrate cells more readily once membrane integrity is compromised, thereby promoting intracellular ROS accumulation (Xu et al., 2021). When ROS levels exceed the scavenging capacity of the cellular antioxidant system, toxic ROS can no longer be effectively removed; moreover, excessive ROS may impair antioxidant enzymes such as superoxide dismutase and catalase, ultimately leading to breakdown of intracellular redox homeostasis (Sun et al., 2014). Ultimately, the intracellular redox homeostasis was broken down. Xu et al. (2021) suggested that $^1O_2$ may diffuse into yeast cells and attack mitochondrial membranes, resulting in depolarization of the mitochondrial membrane potential (Δψm). Loss of Δψm reflects a weakened bioenergetic driving force and can compromise ATP synthesis as well as Δψm-dependent transport processes (Carraro & Bernardi, 2016; Görlach et al., 2015). Transient opening of the mitochondrial permeability transition pore (mPTP) can rapidly dissipate the proton motive force and accelerate Δψm collapse. Excess intracellular ROS may facilitate mPTP opening by oxidizing mitochondrial membrane lipids and/or critical protein complexes, thereby reinforcing Δψm depolarization (Xu et al., 2021). Beyond ROS, reactive nitrogen species may further aggravate mitochondrial injury. In particular, NO and $ONOO^-$ have been suggested to induce mitochondrial dysfunction by inhibiting respiratory complexes (e.g., complexes I, II, and V) and promoting nitration of electron transport–related enzymes (Szabó et al., 2007).

Accordingly, LTP-derived RONS are proposed to disrupt the electron transport chain, the tricarboxylic acid cycle, and cellular ROS-regulatory networks, thereby perturbing redox balance and energy metabolism and ultimately triggering mitochondrial dysfunction (Palma et al., 2024). However, Xu et al. (2021) reported a biphasic ATP response in yeast following plasma exposure, with ATP levels increasing initially and then declining as treatment time extended. The transient ATP elevation may involve Ca^{2+}-mediated metabolic activation, as Ca^{2+} can stimulate enzymes in the Krebs cycle and oxidative phosphorylation, increasing metabolic flux; however, enhanced respiration inevitably increases electron leakage from the ETC, elevating ROS generation (Görlach et al., 2015). With continuous plasma exposure, ROS may accumulate from both plasma-derived oxidants and mitochondrial respiratory processes, ultimately leading to a reduction in cellular ATP (Xu et al., 2021). Oxidative stress and mitochondrial dysfunction may contribute to regulated cell death pathways. The extent of mitochondrial damage and Δψm depolarization has been linked to apoptosis-like processes, whereas more severe mitochondrial injury may promote necrosis-like outcomes (Mattson, 2000).

3.2.1.6.2. Ion homeostasis disruption. Disruption of Ca^{2+} homeostasis has been proposed as one potential mechanism underlying plasma-induced microbial inactivation. Ca^{2+} regulate a broad range of cellular processes and are closely linked to energy metabolism (Wang et al., 2022). Reactive species generated during LTP treatment can oxidize membrane lipids and proteins, weakening the membrane barrier and increasing permeability, thereby disturbing ionic homeostasis (Mahmoud et al., 2025). Wang, Xing, et al. (2023) observed a significant Ca^{2+} leakage after 10 min of LTP etreatment. Because the leakage of intracellular ions is commonly used as an indicator of altered membrane permeability, this result suggests substantial LTP-induced membrane injury. In general, LTP-associated Ca^{2+} leakage is likely attributable to oxidative damage to membrane components together with impaired energy metabolism, which compromises the function of ion channels and pumps and prevents cells from maintaining Ca^{2+} gradients.

Ca^{2+} perturbations may exhibit clear time dependence. In a study investigating fungal inactivation by LTP, Xu et al. (2021) reported that plasma exposure induced a pronounced increase in intracellular Ca^{2+} at early stages. One plausible explanation is the mobilization of intracellular Ca^{2+} stores, implying Ca^{2+} release from internal compartments into the cytosol. With prolonged treatment, intracellular Ca^{2+} levels decreased markedly, which was attributed to progressive loss of membrane integrity and consequent Ca^{2+} leakage (Xu et al., 2021). Such abnormal Ca^{2+} fluctuations can further disrupt electrophysiological status and metabolic processes, promote LTP membrane depolarization (i.e., collapse of the proton motive force), and impair transmembrane transport and ATP homeostasis, thereby accelerating cell death (Molina-Hernandez et al., 2022). Moreover, LTP-derived RONS may trigger endoplasmic reticulum Ca^{2+} release, reinforce mitochondrial Ca^{2+} overload, and promote opening of the mitochondrial pmPTP, leading to dissipation of the mitochondrial membrane potential and suppression of oxidative phosphorylation (Xu et al., 2021). Collectively, these events drive bioenergetic failure and contribute to LTP-induced cell death (Tajeddine, 2016).

3.2.1.6.3. Redox imbalance. As exogenous RONS continuously penetrate cells, the burden on intracellular antioxidant enzymes increases significantly to maintain redox homeostasis and counteract oxidative stress (Wang et al., 2023). RONS generated by LTP react with water to produce additional reactive species and release H^+, thereby lowering the system pH (Zhao et al., 2020). These RONS can damage the active sites of enzymes, oxidize histidine residues and disulfide bonds in antioxidant enzymes, leading to structural impairment and reduced enzymatic activity (Long et al., 2025). As the integrity of the cell membrane deteriorates, intracellular enzymes leak out through newly formed membrane pores. The loss of antioxidant enzymes further exacerbates intracellular oxidative stress, ultimately resulting in a severe disruption of redox homeostasis (Wang et al., 2023). In addition, LTP may exert another inactivation mechanism by inducing programmed cell death (PCD) in bacteria (Liao et al., 2017). Study has shown that short-term exposure (15 s) to LTP can induce apoptotic physiological characteristics in bacteria, indicating that LTP is capable of triggering bacterial PCD (Lunov et al., 2015). This effect may be attributed to excessive ROS and RNS causing oxidative stress in cells, leading to the oxidation of intracellular biomacromolecules and, eventually, cell death.

To gain an in-depth understanding of the physicochemical processes underlying the interactions between LTP and microorganisms, advanced analytical techniques such as ion chromatography, optical emission spectroscopy, and plasma kinetics can be employed to investigate the distribution and active sites of reactive species within microbial cells. In addition, since exogenous microbial contamination may be introduced during food packaging, developing effective strategies to mitigate this risk represents an important direction for future research.

3.2.2. Mechanisms of allergen degradation by LTP

Recent studies indicated that LTP could effectively reduce allergens in peanut (Hsu et al., 2023; Hsieh et al., 2023), milk (Ng et al., 2021; Sharma et al., 2022), egg (Zhang, Ren, et al., 2024), and seafood (Cheng et al., 2023; Zou et al., 2023). Hsu et al. (2023) reported approximately 38% reduction in the Ara h 1 antigenicity binding after 3 min of cold argon plasma treatment. Further increase in treatment time to 15 min resulted in 66% reduction. Ekezie et al. (2019) used direct cold argon plasma treatment on shrimp and reported the reduction in IgE binding to tropomyosin by up to 18% when compared to the control.

Mechanistically, LTP modifies the linear and conformational epitopes of allergenic proteins, reducing their recognition by IgE and significantly lowering their allergenic potential. In the oxidative microenvironment created by LTP, amino acid residues on the allergenic proteins undergo complex chemical modifications, such as nitration, oxidation, hydroxylation, sulfonation, and dimerization (Fig. 8). These changes alter both the surface structure and three-dimensional conformation of the proteins, disrupting IgE binding and alleviating allergic reactions. Through these chemical processes, LTP demonstrates significant potential for allergen desensitization treatments.

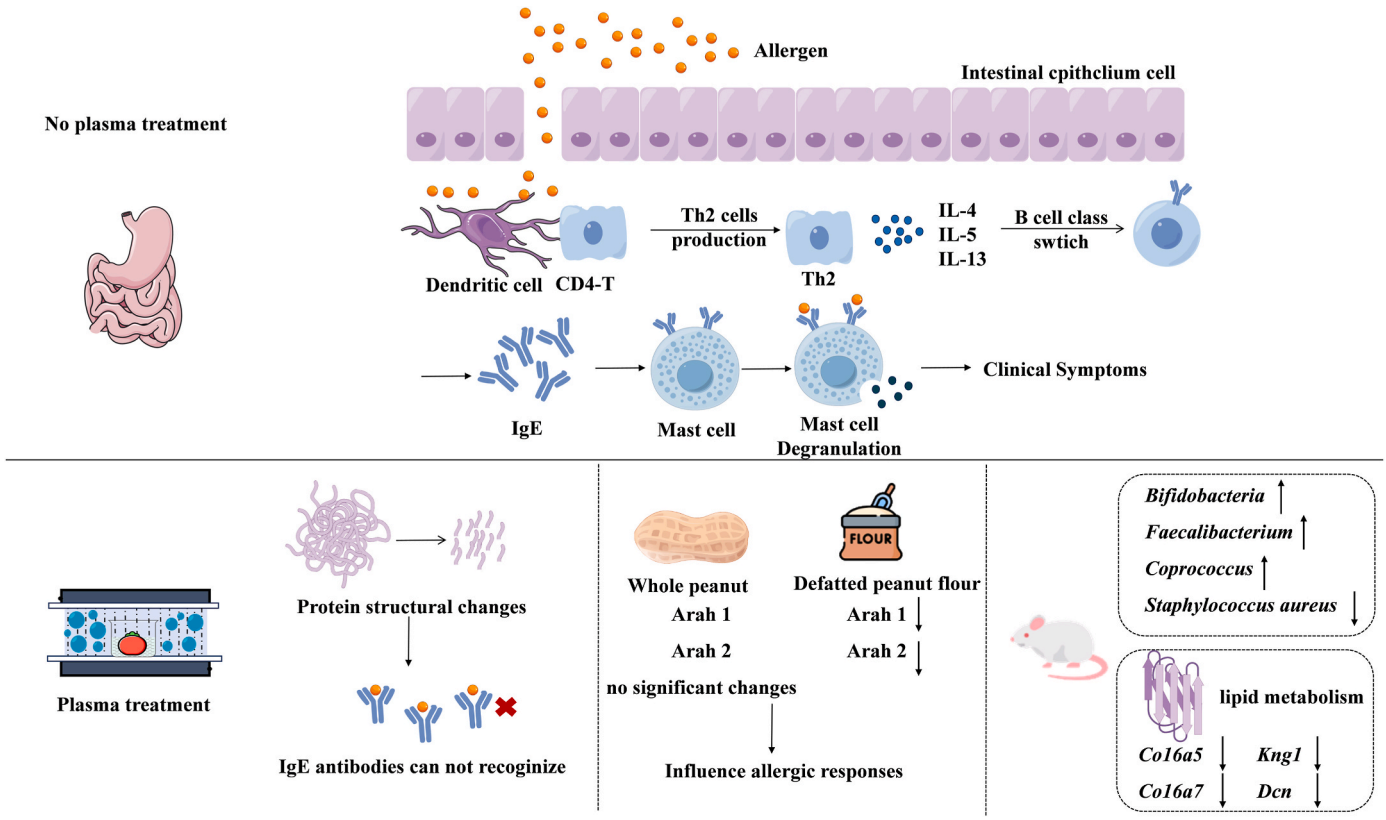

Fig. 8. Degradation Mechanisms of allergen by LTP.

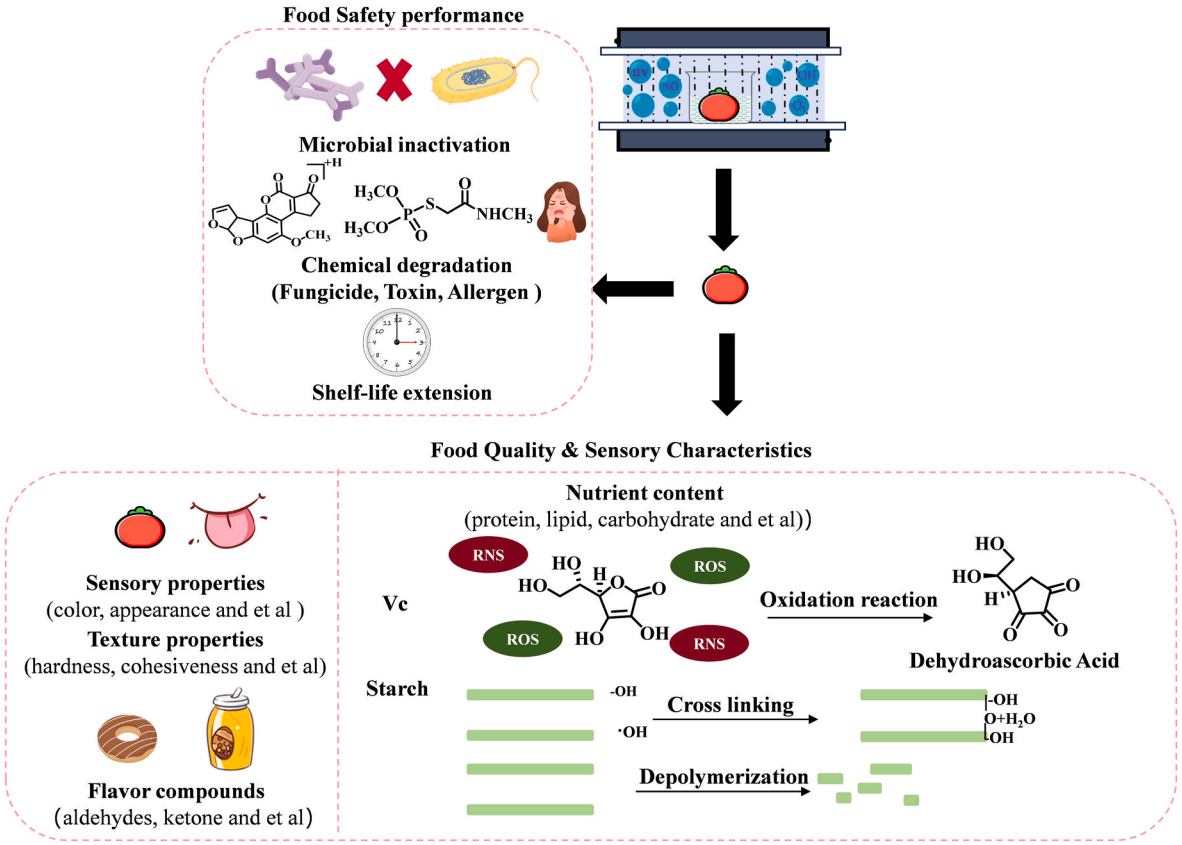

Fig. 9. Plasma-induced effects on sensory quality (e.g., color, texture, flavor) and nutritional components (e.g., vitamin and protein content) of foods. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2.2.1. Protein structural modifications. Protein carbonylation is a typical hallmark of oxidative modification and occurs through three main mechanisms: (1) direct oxidation of amino acid side chains; (2) oxidative cleavage of the peptide backbone; and (3) covalent binding between proteins and reactive intermediates derived from lipid peroxidation or glycation.

3.2.2.2. Amino acid oxidation. The oxidation microenvironment generated by LTP can induce amino acid oxidation, particularly targeting aromatic and sulfur-containing residues. The thiol (-SH) group of cysteine is prone to oxidation, leading to the formation of disulfide bonds while methionine (Met) can be oxidized to form sulfoxide derivatives (Cheng et al., 2023). Additionally, LTP can oxidize Trp residues, triggering carbonylation reactions and producing compounds such as *N*-formylkynurenine (Cheng et al., 2023). Protein carbonylation, a hallmark of protein oxidation, involves structural modifications of amino acid side chains and the introduction of new carbonyl groups. Arginine (Arg) is particularly sensitive to carbonylation. Upon oxidation, Arg can generate glutamyl semialdehydes containing carbonyl groups, which may be further oxidized to Glu (Suzuki, 2019). After the air plasma treatment for 7 min, the α-helix content reduced from 66 to 51% (Hsieh et al., 2023). This result can be attributed to plasma-induced protein oxidation and aggregation. Ultimately, the structural changes induced by LTP treatment alter the functional properties of peanut protein.

3.2.2.3. Peptide bond cleavage. Among ROS,•OH exhibits strong oxidative activity and can oxidize casein, resulting in alterations of conformational epitopes. This process subsequently leads to peptide bond cleavage and fragmentation into smaller peptide segments (Cai et al., 2025). In contrast, longer and more intact peptide chains are more easily recognized by IgE antibodies, thereby triggering a cascade of allergic reactions (Cai et al., 2025). Therefore, the reduction in peptide molecular weight is likely one of the key factors contributing to the observed decrease in antigenicity. Moreover, modifications of conformational epitopes and amino acid sequences also play critical roles in attenuating sensitization (Zeng et al., 2023).

The presence of •OH could cleave the peptide bond of protein, thereby exposing carbonyl groups (Krewing et al., 2020). One of the most relevant consequences of the presence of carbonyl groups is that they can further react with the alpha-amino group of lysine residues. This reaction leads to the formation of intramolecular or intermolecular crosslinks that promote the formation of protein aggregates (Olatunde et al., 2021). Such structural changes often result in reduced protein solubility and may contribute to decreased allergenicity. Simultaneously, hydrated electrons and ROS/RNS generated by LTP can trigger reductive reactions, reducing carbonyl groups on peptide bonds and initiating deamination processes (Pan et al., 2021). Different amino acids exhibit varying sensitivities to these LTP-induced chemical modifications. As the structure of casein changes, its epitopes are altered, impairing their ability to bind specific antibodies and thus reducing antigenicity.

3.2.2.4. Deamidation. Proline (Pro) is particularly susceptible to ring-opening, fragmentation, or addition reactions with hydroxyl or carbonyl groups. Moreover, reactive species such as •OH and O_3 can oxidize amino groups (-NH or -NH_2), thereby lowering the activation energy barrier for deamidation reactions. LTP etching may further expose the amide side chain of asparagine residues, increasing the likelihood of deamidation (Cocco et al., 2007). These structural alterations can lead to side-chain modification, peptide bond cleavage, and the disruption of IgE-binding epitopes, ultimately reducing allergenicity (Qu et al., 2023). Notably, LTP-induced fragmentation of peptide chains at these sensitive sites renders the epitopes unrecognizable by IgE antibodies, effectively diminishing allergic responses.

3.2.2.5. Validation in protein systems

3.2.2.5.1. Tropomyosin (TM). TM is a major allergen in tropical shellfish and exhibits high conformational stability due to its α-helix-rich structure. Study has shown that LTP treatment significantly disrupts the secondary structure of TM, reducing the α-helix content from 69% to 34%, while increasing the β-turn, random coil, and β-sheet content from 16%, 13%, and 2% to 17%, 16%, and 33%, respectively (Zhong et al., 2024). This transition from an ordered to a disordered structure may impair conformational epitopes and reduce allergenicity. In addition, LTP treatment markedly reduces the total and free sulfhydryl content in TM, possibly due to the oxidation of -SH groups to disulfide bonds. Although disulfide bond formation can help maintain tertiary structure, under certain conditions, it may also promote protein aggregation and influence allergenicity. A similar trend has been observed in cow's milk protein allergy, one of the most common food allergies, with a prevalence as high as 6% in western countries and increasing (Caffarelli et al., 2010).

3.2.2.5.2. Casein. Casein, due to its favorable functional properties, is widely used in the food industry. LTP treatment can cause conformational unfolding of casein molecules, exposing buried Trp residues in hydrophobic regions to a polar environment, resulting in fluorescence quenching and non-covalent aggregation of hydrophobic groups (Cai et al., 2025). After 12 min of treatment, a large number of ·OH radicals hydroxylated Trp, further intensifying fluorescence quenching and inducing a red shift in the emission peak. These changes suggest that Trp residues in hydrophobic domains undergo oxidative modification, indicating significant alterations in casein's tertiary structure and a potential reduction in its antigenicity (Cai et al., 2025).

3.2.2.6. Immunomodulatory signaling pathways

3.2.2.6.1. PI3K/Akt/mTOR axis. Alterations in protein structure frequently result in changes to antigenic epitopes, which can subsequently influence IgE-binding LTP acity and modulate downstream signaling pathways. Protein kinase B (PKB/Akt), a serine/threonine kinase and a direct downstream effector of phosphoinositide 3-kinase (PI3K), plays a central role in the PI3K/Akt/mTOR signaling axis (Manning & Cantley, 2007). The mechanistic target of rapamycin (mTOR), a key downstream component of the PI3K/Akt pathway, also functions as a serine/threonine kinase and forms two distinct multiprotein complexes: mTORC1 and mTORC2, each with unique biological functions (Manning & Cantley, 2007). MTOR signaling integrates various micro environmental cues to regulate immune function and T-cell differentiation (Manning & Cantley, 2007). *Col6a5, Col6a6,* and *Epx* have been identified as potential biomarkers associated with TM-induced food allergy. Among them, *Col6a5* and *Col6a6* are involved in the PI3K/Akt pathway and contribute to Dcn-mediated regulation of mTOR phosphorylation, while *Epx* release serves as a hallmark of eosinophilic activation typically observed in allergic asthma (Tang et al., 2024; Zhong et al., 2024). Following LTP treatment, the expression levels of these allergy-related proteins (*Col6a5, Col6a6, Epx, Dcn,* and *Kng1*) were significantly downregulated, resulting in suppression of PI3K/Akt and mTOR pathway activation. Consequently, this led to attenuation of Th2-type immune responses and enhancement of Treg-mediated immunomodulatory activity, thereby alleviating TM-induced allergic symptoms (Zhong et al., 2024).

3.2.2.6.2. Lipid metabolism. LTP may primarily alleviate allergic responses by modulating lipid metabolism-related pathways. Metabolomic analysis revealed a general decrease in the levels of 40 biomarkers following LTP treatment (Zhong et al., 2024). These biomarkers, including linoleic acid, docosahexaenoic acid (DHA), 16-oxohexadecanoic acid, LysoPC (18:0/0:0), and 19S-HETE, are known precursors of bioactive lipid mediators such as oxidized phospholipids (Cai et al., 2025). Not only are they considered potential diagnostic biomarkers for casein allergy, but their reduced levels also suggest that LTP may attenuate allergic reactions by inhibiting the conversion of

membrane lipids into oxidized lipid species. Furthermore, KEGG pathway enrichment analysis revealed significant enrichment of the steroid hormone biosynthesis pathway and the PPAR signaling pathway in the LTP-treated group, indicating that lipid metabolism may play a key regulatory role in the anti-allergic effects of LTP (Cai et al., 2025). Among the differentially expressed genes, *Hsd3b2*, a core component of the steroid biosynthesis pathway, was markedly upregulated after LTP treatment (Cai et al., 2025). Given that steroid biosynthesis represents an important branch of lipid metabolism, this finding further supports the involvement of lipid metabolic pathways in the LTP-mediated alleviation of allergic responses (Mirza et al., 2019). Specifically, PPARα regulates genes involved in fatty acid metabolism and lipoprotein synthesis; PPARγ is associated with adipogenesis and systemic energy metabolism; and PPARβ/δ, which is widely expressed in various tissues, primarily promotes fatty acid oxidation, energy expenditure, and adaptive thermogenesis (Hao et al., 2024).

3.2.2.6.3. Gut microbiota modulation. Food allergens are primarily absorbed in the gut, which hosts a complex and diverse microbiota. Increasing evidence suggests a close relationship between gut microbiota and allergic reactions, with dysbiosis often preceding the onset of allergic inflammation. LTP treatment significantly increased both the species richness and diversity of the gut microbiota, indicating that LTP-treated casein enhances gut microbiota diversity and improves gut health in mice (Cai et al., 2025). LTP may exert its effects by modulating the gut microbiota composition: in LTP-treated mice, the ratio of Firmicutes to Bacteroidetes, which is associated with allergic phenotypes, was significantly reduced. At the genus level, LTP treatment inhibited the proliferation of *Staphylococcus*, a common pathogenic bacterium known to enhance Th2 immune responses and produce δ-toxins that activate mast cells, thus contributing to allergic reactions (Cai et al., 2025).

In addition to directly regulating the microbiota, LTP may also exert an indirect effect by altering the food matrix. LTP treatment induces hydrolysis of peptide chains in casein, releasing bioactive peptides. As an important source of functional peptides, casein-derived bioactive peptides not only inhibit the growth of harmful bacteria but also promote the colonization of beneficial bacteria in the gut. After 12 min of LTP treatment, the abundance of beneficial bacteria such as *Bifidobacteria* and *Coprococcus* reached its highest (Cai et al., 2025). The increase in these bacteria is of significant functional importance: *Bifidobacteria* is associated with reduced allergic reactions, while *Coprococcus* produces butyrate—a key short-chain fatty acid with anti-inflammatory properties that plays a central role in immune modulation and the maintenance of mucosal homeostasis (Lee et al., 2020). These findings highlight the critical importance of investigating gut microbiota dynamics for advancing our understanding of food allergy mechanisms and developing novel therapeutic strategies.

3.2.2.6.4. Matrix effect on allergenicity. The composition of the matrix plays a crucial role in determining the effectiveness of LTP. The specific elements and structure of the matrix significantly impact how well LTP can be induced and maintained, thereby affecting overall neural plasticity and cognitive functions. The precise arrangement and interactions within the matrix are essential factors that critically influence the efficacy of LTP.

Peanut allergy is among the most severe food allergies and a major cause of fatal anaphylactic reactions. Evidence indicates that, under identical LTP exposure (30 min), the antigenicity of major peanut allergens decreases more markedly in defatted peanut flour (DPF) than in whole peanuts (WP): Ara h2 antigenicity was reduced by 30% in WP versus 42% in DPF, while Ara h1 decreased by 36% in WP versus 41% (Venkataratnam et al., 2020). This matrix dependence suggests that lipids, carbohydrates, and other proteins in the food matrix may modulate allergenic potential. In intact matrices, lipids and other constituents may form protective barriers that reduce the effective contact between reactive species and allergenic proteins, thereby attenuating plasma-induced protein modifications (Shah et al., 2019). In addition, polysaccharide–protein, protein–protein, and protein–lipid interactions may remodel protein conformation and mask conformational epitopes, consequently altering IgE recognition and the antigenicity changes reflected by competitive ELISA (Shah et al., 2019). At present, the mechanisms underlying plasma-induced allergen degradation remain incompletely understood. Future studies should prioritize high-resolution analytical approaches to dynamically profile LTP-generated reactive species, identify their specific attack sites on antigenic epitopes, and elucidate the structure–activity relationships linking epitope modifications to reduced allergenicity.

The mechanism underlying plasma-induced allergen degradation remains unclear. Future studies should focus on developing high-resolution analytical methods to dynamically monitor the reactive species generated by LTP, identify their specific attack sites on antigen epitopes, and elucidate the structure–activity relationships between epitope modifications and reduced allergenicity.

4. Toxicology and quality impact of LTP-treated foods

4.1. Toxicological safety

Although LTP has demonstrated high efficiency in degrading pesticide residues, microbial contaminants, and allergens, its application inevitably generates ROS/RNS, ultraviolet photons, and charged particles, which may interact with food components or biological systems. Therefore, evaluating the possible toxicity of LTP-treated foods is key to guaranteeing safe process development and commercial application in the food industry.

4.1.1. In vitro safety evaluation

Bisphenols are recognized as toxic compounds posing potential risks to both the ecological environment and public health. The effects of BPA, BPS, and their transformation products (TPs) generated during LTP exposure on the viability of HepG2 cells after 24 h treatment were systematically evaluated (Kovačič et al., 2023). The results demonstrated that none of the tested bisphenols or their TPs induced significant alterations in cell viability. However, after 8 min of exposure, a time-dependent increase of 30% in mitochondrial dehydrogenase activity was observed in cells treated with BPA and its TPs compared to the control group (Kovačič et al., 2023). This finding suggests that the transformation products of BPA may trigger a cellular stress response mechanism, potentially mediated by their underlying toxicity. Moreover, the duration of plasma treatment significantly affected cell growth. When supplemented with 10% v/v lettuce broth treated with LTP for 1 min, cell growth decreased to 74% of the untreated control. When the treatment time was extended to 10 min, cell growth remained stable after an initial decrease, reaching 68% of the untreated control (Heslin et al., 2020).

4.1.2. In vivo safety evaluation

4.1.2.1. Mammalian models. The mammalian safety evaluation of LTP technology has established a multilayered toxicological evidence framework. As the hematopoietic stem cell system is an important susceptible target of toxic compounds, it is used in evaluating the physiological and pathological status of humans and animals. Analysis of whole blood for hematological parameters demonstrated that none displayed a significant difference between the control and LTP-treated grape tomatoes (Lee et al., 2023). The results were uniform in both the acute and subacute tests. The lack of any significant variation in toxicity confirmed the safety of LTP treatment.

Total bilirubin, aspartate aminotransferase, and alanine aminotransferase levels are used as representatives of hepatocellular damage, whereas blood urea nitrogen and creatinine act as biomarkers of nephrotoxicity. In the acute toxicity assay, blood urea nitrogen and

triglyceride levels were slightly higher in the control group than in the LTP-treated group among female SD rats. In males, only the total protein was slightly increased in the LTP-treated group than in the control group (Lee et al., 2023). In the subacute toxicity assay, the total bilirubin and total protein levels varied significantly in the male group only, but the levels were within a normal range, indicating a lack of toxicity. Kim et al. (2016) fed mice with emulsion-type sausages cured with LTP-treated water and observed no signs of inflammation compared to the control group. Intestinal length, an established marker of inflammation, typically shortens in response to inflammation. However, no significant differences in intestinal length were observed in mice fed with plasma-treated water-cured emulsion-type sausages. Han et al. (2016) conducted an acute toxicity test on rats exposed to a single dose (5000 mg/kg) of edible film treated with LTP. The rats did not exhibit increased mortality, adverse clinical signs, or abnormal changes in body weight, macroscopic features, or food consumption patterns. No deaths were observed, and the animals exhibited normal behavior throughout the study. Dobrynin et al. (2011) demonstrated that LTP did not induce toxic effects on pigskin wounds. On the contrary, LTP appeared to enhance blood clotting, thereby protecting wound tissue from the damaging effects of cold plasma exposure. These studies collectively suggest that plasma treatment may not induce significant toxic effects and, in some cases, may even offer protective benefits.

4.1.2.2. Aquatic organisms. Zebrafish is a widely recognized aquatic model organism, particularly favored in toxicological research due to its transparent embryos, rapid development, and genetic similarity to humans. Miguel et al. (2025) evaluated the toxicity of plasma-treated cashew apple juice on zebrafish embryonic development at different frequencies (400 Hz and 550 Hz) and concentrations (10 μg/mL and 100 μg/mL). The results showed that, in all treatment groups, the survival rate exceeded 90% at 96 h post-fertilization, and no morphological changes were observed in embryos or larvae. The potential toxicity of LTP to other aquatic species and food types requires further investigation. Future studies should explore its effects on aquatic organisms and its ecological risks in real-world environments.

4.1.2.3. Invertebrate species. Wastewater management represents a major environmental sustainability challenge in the food industry. Acute toxicity assays using *Daphnia magna* indicate that the ecological impact of LTP-treated wastewater is concentration-dependent and operationally manageable. While short-term exposure (24 h) to effluents treated for 5–10 min resulted in significant toxicity reduction (73–100%) at low concentrations, residual toxic effects were observed after 48 h at concentrations up to 10% (Patange et al., 2018). These findings underscore that with optimized treatment parameters and appropriate dilution, LTP technology can effectively reduce wastewater risks while maintaining an acceptable ecotoxicological safety profile for aquatic organisms.

4.1.2.4. Vertebrate species. A comprehensive genome-wide DNA methylation map in chickens revealed patterns that closely resemble those found in classic vertebrates (Li et al., 2011). Zhang et al (2018b) demonstrated that LTP treatment improved the male chicken reproductive system, including increased testosterone levels and sperm quality, with no significant effects on the female reproductive system (estradiol and progesterone levels, egg-laying rate, and egg weight). Additionally, the study found that sperm motility in chickens improved within 40 s of exposure to 11.7 kV LTP, peaking at 20 s. Compared to the control group, there were no significant differences in sperm motility, acrosome integrity, DNA integrity, and total fertility in the LTP-treated group. However, when the exposure time exceeded 60 s, sperm quality significantly decreased, indicating a time-dependent effect of plasma treatment on sperm quality (Zhang et al., 2018a). LTP may also improve growth metabolism by regulating ROS homeostasis in chickens, as well as increasing the expression of GH-IGF1 and its receptors, thyroid hormones, and ATP levels (Zhang et al., 2018c)).

The effectiveness of LTP treatment is highly dependent on processing equipment, operational methods, and specific process parameters, including treatment time, gas flow rate, voltage, power input, current, and the distance between the electrodes and the sample. Significant variations in cytotoxicity and ecotoxicological endpoints occur under different processing conditions and plasma-generation gas environments. The cytotoxicity induced by LTP is primarily attributed to the generation of hydrogen peroxide, which synergizes with other plasma-derived reactive components, such as peroxynitrite and peroxynitrous acid (Boehm et al., 2018).

Although direct evidence regarding the toxicity of cold plasma remains limited, the generation of RONS during the treatment process, which have been associated with chronic liver diseases and other specific conditions, continues to raise concerns about the safety of plasma-treated food (Che et al., 2023). While LTP technology holds significant potential for improving food safety and extending shelf life, its commercialization faces regulatory challenges, primarily due to the lack of a unified legal framework. This underscores the necessity of conducting rigorous toxicological assessments, supported by real-time monitoring, to ensure compliance with existing safety standards.

Currently, research on the toxicological assessment of LTP-treated food remains scarce. The reactive species generated by LTP may be associated with various chemical changes in food, including modifications of amino acids in proteins, oxidation of high molecular weight compounds into organic acids, and secondary metabolism during lipid peroxidation. The toxicological safety assessment of these secondary metabolites should not be overlooked (Muhammad et al., 2022). To establish a regulatory system based on scientific evidence and ensure consumer safety, comprehensive studies, including oral toxicity testing and long-term health impact assessments, are urgently needed. Such work is crucial to verify the safety of products before the application of LTP technology in the food industry.

4.2. Impact on food quality

LTP is increasingly regarded as a promising alternative in the field of food processing and preservation. LTP preserves sensory, textural, and nutritional properties better than thermal/chemical methods (Fig. 9).

4.2.1. Sensory & physical attributes

4.2.1.1. Color stability. Studies have shown that LTP treatment can effectively delay quality deterioration in foods. Mishra et al. (2024) showed that LTP treatment of Red Globe grapes helped preserve the red coloration throughout storage, thereby sustaining a more consistent appearance and overall visual quality. The color properties of fruits primarily depend on browning reactions and the degradation of anthocyanins. LTP treatment may slow down these processes through its antioxidative effects, reducing oxidation reactions that lead to browning and loss of color stability. Active species generated by LTP, such as ROS and RNS, play a crucial role in slowing down the oxidation of phenolic compounds, thereby maintaining color and nutritional content. Additionally, LTP treatment may inhibit the activity of key enzymes, such as polyphenol oxidase, thus reducing browning reactions and preserving the color and quality of the food. In another study, triple-cycle LTP (3 × 1 min) effectively reduced black spots in shrimp and extended acceptable sensory scores to Day 4 of refrigeration (Hu et al., 2023). This result can be attributed to the reduction in microbial growth and the inhibition of enzymatic activity responsible for food spoilage. The prolonged O_3 exposure in the LTP cyclical treatment mode promoted O_3 penetration into the red shrimp muscles, further benefiting food preservation.

4.2.1.2. Texture modification. In terms of texture improvement, LTP treatment also shows notable potential in aligning food texture more

closely with consumer preferences. Brown rice treated under the conditions of 1 kHz frequency, 70% duty cycle, 28 kV voltage, and 15 min of exposure exhibited significant reductions in hardness and viscosity, resulting in a texture more similar to that of white rice while retaining high nutritional value (Yang et al., 2024). This improvement may be attributed to enhanced solute dissolution and water penetration during cooking following LTP pre-treatment.

Natural starches have certain application limitations due to their viscosity, process tolerance, and thermal stability. LTP-induced starch modification can improve the solubility, expansion, and digestibility of starch, thereby enhancing the texture and mouthfeel of foods. A study by Okyere et al. (2019) found that LTP-treatment with carbon dioxide-argon radio frequency LTP resulted in lipid oxidation in waxy starches, generating free fatty acids. These free fatty acids may form complexes with starch granules, leading to a reduction in peak viscosity. In addition, the gelation enthalpy of the treated starch increased significantly, and the content of amylose also showed a marked increase. The increase in amylose content after LTP treatment is primarily attributed to plasma-induced cross-linking between starch polymer chains, initiated by free radicals and high-energy electrons generated during plasma discharge (Muhammad et al., 2018). Cleavage of hydroxyl groups (C–OH) at the reducing ends facilitates the formation of new C–O–C linkages through dehydration reactions, resulting in effective intermolecular cross-linking (Muhammad et al., 2018). Thirumdas et al. (2017) identified the C-2 position of glucose as the most reactive site for this process. Concurrently, ·OH derived from water decomposition or atmospheric oxygen may cleave glycosidic bonds, generating shorter linear fragments that also contribute to the apparent amylose content. Moreover, increased plasma intensity and exposure duration enhance hydroxyl dipolarity, enabling charged reactive species to penetrate the helical cavities of starch and promote further cross-linking, leading to structural reorganization and an overall rise in amylose content (Sudheesh et al., 2020; (Ma & Jiang, 2024)).

Such structural modification not only improves food texture and extends shelf life but also offers new strategies for developing functional starches with better adaptability to various processing conditions such as baking and freezing, highlighting the great application potential of LTP technology in starch structural modification and functional enhancement.

4.2.2. Nutritional components

Although LTP technology generally has minimal impact on sensory attributes, physicochemical properties, and nutritional content during food processing, it may still cause unavoidable losses of certain nutrients.

4.2.2.1. Vitamin C. Most studies on cold plasma effects on food systems focus on vitamin C stability. Leite et al. (2021) reported that LTP treatment at 200 Hz increased vitamin C content in cashew apple juice from 637.9 mg/L to 820.6 mg/L and 825.7 mg/L, a 28% and 29% increase, respectively, likely due to the activation of dehydroascorbate reductase, which reduces dehydroascorbic acid to ascorbic acid. However, intense treatment conditions, such as prolonged exposure or high discharge power, can break chemical bonds in the vitamin C molecule and exacerbate degradation (Fernandes et al., 2021; Vedaei et al., 2021). Hosseini et al. (2020) found a 21% decrease in vitamin C content in sour cherry juice after 8 min of LTP treatment at 49 kV/cm field strength and 0.7 cm gap, likely due to ozone-derived ozonides or reactions with singlet oxygen and free radicals.

Mild LTP conditions (short duration, low intensity) tend to induce beneficial stress responses, maintaining or enhancing vitamin C content, while high-intensity conditions cause irreversible oxidative damage. These findings highlight the complex effects of LTP on food composition, strongly influenced by the food matrix and processing parameters.

4.2.2.2. Phenolic compounds. LTP can induce both an increase and a decrease in phenolics. Medvecká et al. (2020) observed that total polyphenolic content rose from about 6.7 g/100 g to 8.3 g/100 g of spice berries sample following 5 min of LTP treatment, representing an increase of roughly 24%. LTP may elicit plant defense responses, which are often accompanied by upregulated energy metabolism (e.g., increased ATP production) and accelerated sugar utilization, thereby promoting the biosynthesis of phenolic compounds (Li et al., 2019). In addition, plasma-derived ROS/RNS may partially compromise cell membranes and induce cytoplasmic leakage, thereby enhancing the release and extractability of phenolic compounds (Illera et al., 2019). Additionally, the increase in phenolic content could also be due to the depolymerization of tannins (Gamaleev et al., 2020). In plants, ROS and UV radiation act as abiotic elicitors, playing a role in the regulation of plant stress responses. These stress regulators mediate phenolic content during the stress response, contributing to the increase in phenolics (Gamaleev et al., 2020). Li et al. (2019) reported that LTP treatment at 50 Hz and 60 kV for 5 min reduced the phenolic content in pitaya by 17%. This effect is attributed to the generation of energetic electrons during LTP, which dissociate oxygen molecules upon collision. The resulting single oxygen atoms subsequently react with molecular oxygen to form O_3. The presence of O_3 and other reactive species during treatment contributes to the degradation of phenolic compounds. Specifically, O_3 attacks the aromatic rings of phenolics, producing aliphatic derivatives such as hydroxylated and quinone compounds, which cause structural disruption and breakdown (Sruthi et al., 2022). Another proposed mechanism involves the hydroxylation of benzene rings within phenolic structures. Reactive species facilitate the formation of hydroxycyclo carbonyl radicals, which initiate a cascade of reactions, ultimately leading to a decline in total phenolic (Sruthi et al., 2022).

The choice of LTP processing parameters significantly influences food quality (Oner et al., 2023). Excessive treatment intensity may lead to the degradation of nutrients and deterioration of sensory attributes, posing a challenge to maintaining overall product quality (Herianto, Hou, Lin, & Chen, 2021; Gavahian et al., 2024). Excess plasma-generated reactive species induce lipid and protein oxidation, producing secondary reaction products that exacerbate off-flavor development in pork. Therefore, finding an optimal balance between microbial safety and food quality preservation is a key focus for future research. Moreover, the underlying mechanisms remain to be further explored, particularly the physicochemical and molecular pathways induced by plasma during food processing.

5. Limitations and challenges for LTP development

Although LTP operates at low temperatures and enables rapid, energy-efficient processing with potent antimicrobial efficacy while minimally affecting food quality and the environment, several limitations still restrict its broader adoption in the food industry (Bourke et al., 2018). Reactive species in LTP are generally generated at atmospheric or near-atmospheric pressure via gas discharges driven by kV-level high voltages and strong electric fields, which increases upfront installation costs and can lead to relatively high maintenance requirements during long-term operation. In addition, plasma systems intended for food processing should be easy to operate, require minimal upkeep, and accommodate multiple working gases; however, given the slim profit margins in the food sector, reducing operating expenditures by avoiding expensive noble gases (e.g., He and Ar) is often a practical constraint (Gavahian & Khaneghah, 2020).

Furthermore, the sterilization/degradation performance of LTP is highly sensitive to reactor configuration and processing parameters, including the type of plasma-generating device, the composition of the excitation gas, the applied voltage, and the treatment time. These factors collectively determine the reactive species profile and energy input, thereby markedly influencing LTP efficiency and treatment outcomes (Zhang et al., 2023). While relatively uniform discharges can be readily

achieved at laboratory scale due to small sample volumes, limited treatment areas, and well-controlled conditions, industrial-scale continuous and large-area processing is challenged by the heterogeneity of food matrices (e.g., surface topography, moisture variations, and organic load), which often necessitates matrix-specific parameter optimization and consequently complicates standardized implementation.

Finally, although some studies under specific experimental conditions have suggested no obvious toxicity associated with LTP treatment (Rutkowski et al., 2020), a more robust evidence base is still required to support its safety profile and regulatory acceptance. In particular, excessively high discharge voltages may reduce energy-utilization efficiency and increase the formation of by-products such as O_3 and nitrogen oxides (NOx) (Katsigiannis et al., 2022), raising occupational exposure concerns and potentially inducing oxidation- and nitration-related chemical changes in treated matrices. Therefore, systematic safety assessments of gas-phase by-products, food quality changes, and potential impacts on human health remain necessary to facilitate regulatory approval and industrial deployment.

6. Conclusion

LTP is a non-thermal intervention that has been applied to reduce major chemical and biological contaminants in foods, including pesticide residues, microorganisms, mycotoxins, and food allergens. Its performance is primarily governed by plasma-derived reactive species and associated physicochemical effects (e.g., electric fields and UV emission), which drive pesticide degradation, microbial inactivation, and toxin/allergen modification. Meanwhile, under appropriate conditions, LTP may maintain color stability, texture, and nutritional properties of foods. Although substantial progress has been made in understanding its mechanisms and applications, challenges persist in optimizing processing parameters to balance efficacy and quality across various food matrices. Future research should concentrate on elucidating the detailed interactions between LTP-generated reactive species and food macromolecules, as well as evaluating the long-term safety and regulatory implications of LTP-treated foods. Multidisciplinary collaboration among food science, engineering, and toxicology is essential to harness the advantages of LTP, including environmental compatibility, residue-free operation, and minimal impact on quality. Furthermore, it is crucial to transform these advantages into scalable industrial applications. Overall, ongoing multidisciplinary efforts are essential to fully realize the benefits of LTP technology and promote its sustainable implementation in food processing.

CRediT authorship contribution statement

Jun Yan: Writing – review & editing, Methodology. **Xue Yuan:** Validation, Data curation. **Marie-Laure Fauconnier:** Methodology. **Xiaoming Fang:** Resources, Formal analysis. **Zhiqiang Kong:** Writing – review & editing, Resources, Data curation. **Lin Li:** Resources, Data curation. **Bei Fan:** Validation, Resources, Project administration, Conceptualization. **Jesus Simal-Gandara:** Resources, Formal analysis. **Minmin Li:** Writing – review & editing, Visualization, Project administration, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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Data availability

No data was used for the research described in the article.

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