

Review

Applications of Atmospheric Pressure Non-Thermal Plasma to Plant Stress Regulation and Animal Health Improvement

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Abstract

Atmospheric pressure non-thermal plasma (APNTP) is an emerging technology with demonstrated potential for mitigating diverse environmental stresses in agriculture and animal health. This review synthesizes current evidence on plasma-mediated stress regulation in plants and animals. For plants, APNTP enhances tolerance to drought, salinity, temperature extremes, heavy-metal toxicity, and pathogen infections through activation of antioxidant systems, stress-responsive gene expression, and adaptive signaling pathways. For animals, APNTP promotes wound healing, microbial disinfection, reproductive health, and environmental pollutant degradation via modulation of oxidative balance, inflammatory responses, and cellular repair mechanisms. However, most reported effects to date are based on laboratory-scale studies under controlled conditions, and critical gaps remain in dose-dependent toxicity profiles, protocol standardization, and long-term safety data. We highlight future priorities including mechanistic studies, parameter optimization, safety assessment, and scalability evaluation. This review provides a comprehensive framework for advancing APNTP applications toward sustainable agriculture and improved animal welfare.

Keywords: atmospheric pressure non-thermal plasma; plant; animal; stress regulation; environment



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1. Introduction

With global climate change intensifying and environmental pollution increasing, biological systems are facing unprecedented environmental pressures [1]. These pressures significantly affect the stability of agricultural production systems, including animal husbandry and crop cultivation [2]. Crop plants are susceptible to a variety of environmental stresses during their growth and development, and unfavorable environments are the main cause of reduced crop yields [3]. Surveys indicate that a 1% increase in agricultural yield translates into a 0.6–1.2% decrease in the absolute number of poor households worldwide [4]. In addition, animal husbandry has been seriously affected by climate change and environmental degradation in recent years. In industrial feeding environments, exposure to ammonia increases the probability of respiratory disease in animals by 15–20% [5]. Heavy-metal contaminants can be enriched through the food chain, ultimately affecting meat

safety [6]. Pathogenic microorganisms increase disease prevalence in animals, reducing growth performance and reproductive efficiency [7]. Heat stress causes dairy cows to experience elevated body temperatures, which can impact their reproductive performance, including hormonal imbalances, reduced oocyte and semen quality, and decreased embryo development and survival [8]. A study on European farms found that heat stress can cause a 2.8% decrease in milk production and a 5.4% loss in monthly income [8]. Meanwhile, the global population is predicted to grow to 9.7 billion by 2050, necessitating an increase of approximately 70% in food production to meet the demands of this population [4]. Reduced production of staple crops (wheat, corn, and rice) and damage to the livestock industry could have serious consequences, including exacerbating global food shortages, poverty, and hunger.

Technical innovations are needed to overcome recent crises in agricultural practices. Atmospheric pressure non-thermal plasma (APNTP) technology developed in physics has received attention in recent years as a potential tool for fostering adaptations to changes in climate and agricultural environments. Plasma is an ionized gas, often referred to as the fourth state of matter, alongside solids, liquids and gases [9,10]. In the plasma state, gas molecules are ionized, producing a mixture of positively charged ions and free electrons, along with neutral particles [11]. Plasmas can be divided into various types based on their temperature, density, and specific properties, including thermal, non-thermal or cold; high-density; and low-pressure plasmas [12]. Among these, APNTP is considered the most suitable type for biological applications due to their ability to generate and sustain plasma at atmospheric pressure [13]. The overall gas temperature remains close to ambient temperature, despite the high energy of the electrons in APNTP [14]. Various types of APNTP are being actively researched for their industrial applications (Figure 1). Volume dielectric barrier discharge plasma (VDBD) systems generate spatially uniform plasma over large areas, making them well suited for seed and grain treatment, but have limited penetration into three-dimensional targets [15–17]. Surface dielectric barrier discharge plasma (SDBD) devices produce surface-confined plasma useful for flow-through decontamination, though penetration depth is shallow [18]. Floating-electrode barrier discharge plasma (FE-DBD) systems use the biological target as the grounded electrode, maximizing direct delivery of RONS but introducing variability across substrates [16]. Atmospheric pressure plasma jet (APPJ) generate stable discharges and enable precise localized treatment control, but their small plasma plume limits the active treatment zone and makes large-scale application challenging [18,19]. Corona discharge systems are simple and low-cost but generate non-uniform plasma with limited RONS output [20,21]. Microwave plasma sources produce high-density RONS but require complex infrastructure, restricting their current use to laboratory or industrial-scale settings [21]. The selection of plasma generation devices fundamentally determines the resulting biological effects, as different devices generate distinct profiles of reactive species, temperature, electric fields, and UV emission. The results showed that SDBD required shorter exposure times than remote plasma sources due to higher plasma density in direct configurations [22]. For Aldrin degradation, corona discharge plasma achieved the highest performance compared with DBD plasma [23]. Therefore, device selection should be guided by the target application and biological system.

To date, APNTP has been used in medicine and agriculture. Medical applications include sterilization of medicine materials and human living tissues, assisting blood coagulation, chronic foot, leg ulcers, wound healing and tissue regeneration [24–26]. Plasma also shows positive effects on the growth, development and crop yield under optimized treatment conditions [27–29]. Many plant seeds are subjected to a pre-sowing plasma treatment to increase the likelihood of timely and uniform germination, including radish

(*Raphanus sativus*), carrot (*Daucus carota sativus* L.), soybean (*Glycine max*), bean (*Phaseolus vulgaris*), mung bean (*Vigna radiata*), black gram (*V. mungo*), pea (*Pisum sativum*), lentil (*Lens culinaris*), peanut (*Arachis hypogaea*), alfalfa (*Medicago sativa*), chickpea (*Cicer aruetinum*), blue lupine (*Lupinus angustifolius*), Egyptian clover (*Trifolium alexandrinum*), fenugreek (*Trigonella foenum-graecum*), and mimosa (*Mimosa pudica*, *M. caesalpiniafolia*) [30,31]. For animal health, plasma treatment can achieve a microbial disinfection efficiency of more than 90% [32] and a wound healing rate of more than 60% under specific experimental conditions [33]. In addition, it can also improve the sperm motility of animals and improve reproductive efficiency [34]. Furthermore, due to its ability to effectively inactivate microorganisms and enzymes, APNTP can also be used as a disinfectant in food packaging, thereby preserving the freshness and extending the shelf life of food [35–38]. It is important to note that these effects are highly dependent on plasma dose, exposure duration, plasma source type, target species, tissue characteristics, and environmental condition.

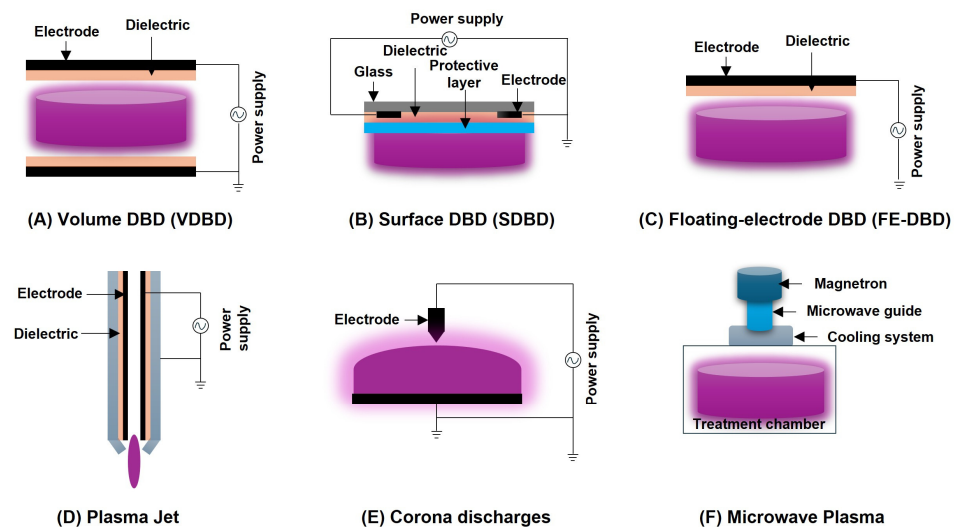


Figure 1. Schematic drawing of diverse atmospheric pressure non-thermal plasma (APNTP) devices.

Currently, plasma has demonstrated its potential in fostering adaptations in plants and animals to climate and agricultural environmental changes. Although studies have shown that animals and plants treated with APNTP are more resistant to biological and abiotic stresses, the outcomes of these treatments vary depending on the animal and plant species, plasma devices, and environmental stresses, and the underlying regulatory mechanisms are still poorly understood [39]. In this review, we summarize and discuss case studies evaluating the improvement in animal and plant resistance through plasma under different environmental stresses and the relevant regulatory mechanisms to examine whether plasma technology can be a promising tool for solving environmental problems.

2. Plasma-Mediated Responses to Environmental Stress in Plants

Plasma agriculture is an emerging field in recent years, particularly in improving plant stress resistance [40]. Plant stress regulation involves the mechanisms and responses that plants employ to cope with adverse environmental conditions, ensuring their survival and productivity. Currently, environmental stresses that affect plant growth and development mainly include drought, salinity, extreme temperatures, nutritional deficiencies, metal toxicity, and biotic stresses such as viral, bacterial, and fungal infections (Figure 2). Studies have demonstrated that plasma can enhance the tolerance of plants to various environmental stresses by activating antioxidant systems, promoting expression of defense-related genes, and regulating plant hormonal and physiological responses and signal transduction (Table 1).

Table 1. Summary of tolerance to stresses and underlying mechanisms in plants induced by atmospheric pressure non-thermal plasma.

Stress	Plant	Type of Plasma (Parameters)	Effects on Plants and Mechanisms	Ref.
Drought	Rapeseed (<i>Brassica napus</i> L.)	Capacitive coupled plasma (CCP; 13.56 MHz, 100 W)	- Enhances seed germination (6.25%) and seedling growth (dry weight of shoots and roots, length of shoots and roots, and lateral root number were significantly increased by 16.67%, 20.22%, 42.72%, 19.09% and 29.12%); - Increases SOD (17.71%) and CAT (16.52%) expression (antioxidant defense) (vs. drought-only control).	[41]
	Wheat seeds (Xiaoyan 22)	Atmospheric dielectric barrier discharge plasma (13.0 kV, 50 Hz, air, 4 min)	- Alleviates adverse effects on seed germination (17.3%) and seedling growth (root length and shoot length increased by 20.0% and 31.9%) and proline content (12.7%); - Decreases MDA content (12.8%), H₂O₂ content (23.1%), and O₂⁻ content (21.5%); - Increases SOD, POD (34%) and CAT activity (antioxidant defense); - Enhances expression of drought resistance-related genes (<i>LEA1</i>, <i>SnRK2</i>, and <i>P5CS</i>) (gene expression and epigenetic regulation). - Increases proline and ABA accumulation (37.9%) (hormonal regulation signaling) (vs. drought-only control)	[42]
	Wheat seeds	High-voltage electrical discharge (HVED; 30 kV, 30 Hz, 30 s, 2 cm)	- Improves germination percentages (16.75% higher in Bernarda vs. Tena), drought resistance germination index, and drought tolerance indices for shoots (28%) and roots (45%) (vs. drought-only control).	[43]
	Barley seeds (<i>Hordeum vulgare</i> L.)	Dielectric barrier discharge plasma (8.6 kV, 1 kHz, 5.3 W, 6.5 mA, air, 3 min)	- Promotes seed germination and first stages of growth (number of roots increased by 20%, root length increased by 70%, and root diameter increased by 80%) (vs. drought-only control); - Increases chlorophyll a and b contents (growth and yield response).	[44]
	Licorice seeds (<i>Glycyrrhiza</i>)	Surface dielectric barrier discharge (SDBD; 20 kV, 6.2 kHz, air and argon at 4.0 L/min, 5 min)	- Accelerates germination speed and efficiency (increased the germination rate by 66%) (vs. drought-only control); - Increases the activity of catalase (CAT) and ascorbate peroxidase (APX) in the treated seeds (antioxidant defense).	[45]

Table 1. Cont.

Stress	Plant	Type of Plasma (Parameters)	Effects on Plants and Mechanisms	Ref.
Salinity	Wheat (<i>Triticum aestivum</i> L.)	Non-thermal plasma	- Enhances shoot fresh and dry mass and total leaf area; - Impacts of salinity on chlorophyll contents are mitigated by plasma; - Increases PAL and peroxidase activity (15%) (antioxidant defense); - Induces expression of heat shock factor A4A (gene expression and epigenetic regulation) (vs. untreated control); - Enhances chlorophyll contents (growth and yield response).	[46]
	Rice (<i>Oryza sativa</i> L.)	Cold plasma	- Improves seed germination and seedling growth, photosynthetic pigments and photosynthetic gas exchange; - Reduces Na⁺ accumulation and increases K⁺ and Ca²⁺ contents in plant cell; - Increases the activities of antioxidant enzymes (SOD, POD, CAT, and APX) and non-antioxidant enzymes (GR, GSH, and GSSG) (antioxidant defense) (vs. salinity-only control); - Enhances chlorophyll and upregulates secondary metabolism-related enzyme activity (PAL, PPO, SKDH, CAD, SuSy, SPS, and AI) (growth and yield response).	[47]
	Wheat seeds	High-voltage electrical discharge (HVED; 30 kV, 30 Hz, 30 s, 2 cm)	- Increases index values of germination salt tolerance (vs. untreated control); - Increases salt tolerance shoot index (50%) and salt tolerance root index (27%) (Bernarda vs. Tena, both HVED-treated).	[43]
	Rice (<i>Oryza sativa</i> L.)	Argon non-thermal plasma (15 Kv, 120 s, argon)	- Increases the germination rate of Longdao 5 (LD5) rice seeds; - Enhances the activity of antioxidant enzymes catalase and SOD (antioxidant defense); - Induction of chitinase and xylanase inhibitory protein expression (inactivation of pathogens) (vs. alkaline stress only control).	[48]
	Cowpea seeds	Low-pressure capacitively coupled non-thermal plasma (CCP-NTP; 250 V, 13.56 MHz RF power, air, 1.0 and 2.0 min)	- Enhances forage productivity and in vitro traits of cowpea cultivated in salty soil (vs. salt-only control); - Enhances relative chlorophyll content (1.29-fold), seedling length (1.91-fold) and fresh weight (1.90-fold) (vs. untreated control); - Increases the total amount of volatile fatty acid and dry matter degradability (9.04%) (growth and yield response) (vs. salt-only control).	[49]

Table 1. Cont.

Stress	Plant	Type of Plasma (Parameters)	Effects on Plants and Mechanisms	Ref.
Salinity	<i>Prosopis koelziana</i>	Dielectric barrier discharge (DBD; 10 kV, air, 0–10 min)	- Germination rates significantly increased (56%), and seeds exhibit enhanced permeability to water and gases; - Activities of enzymes catalase (CAT), ascorbate peroxidase (APX), and guaiacol peroxidase (GPX) increase, while activity of polyphenol oxidase (PPO) decreased (antioxidant defense) (vs. salt-only control).	[50]
	Cotton seed	Dielectric barrier discharge (38 kV, 1 kHz, air, 3 min; 11 kV, 1 kHz, argon, 27 min)	- Increases water absorption of seed and improves warm germination, metabolic chill test germination and chilling tolerance in cotton (vs. untreated control).	[51]
	Tomato seedlings	Cold plasma (CP)	- Induces upregulation of H₂O₂ and ABA cascade signaling, enhancing cold resistance in tomato plants (ROS/RNS signals) (vs. cold-only control).	[52]
Temperature extremes	Rice seeds (<i>Oryza sativa</i> L.)	Dielectric barrier discharge device	- Improves germination of rice seeds affected by heat stress; - Upregulates amylase genes (OsAmy1A, OsAmy1C, OsAmy3B, and OsAmy3E) (gene expression and epigenetic regulation); - Downregulates genes involved in ABA biosynthesis (OsNCED2 and OsNCED5) and upregulates genes involved in ABA catabolism (OsABA8'OH1 and OsABA8'OH3) (hormonal regulation) (vs. heat-only control).	[53]
	Barley seeds (<i>Hordeum vulgare</i> L.)	Dielectric barrier discharge plasma (8.6 kV, 1 kHz, 5.3 W, 6.5 mA, air, 3 min)	- Increases seed germination rate (15%); - Enhances carotenoid accumulation and reduces proline concentration (50%) (antioxidant defense) (vs. cold-only control).	[44]
	Rice seeds (<i>Oryza sativa</i> L.)	Dielectric barrier discharge plasma (13.9 kV, 15.0 kV, and 19.7 kV; argon; 5 L/min; 30 s)	- Improves rice seed germination rates and promotes seedling growth; - Enhances activity and expression of antioxidant enzymes (superoxide dismutase (SOD), catalase (CAT) and peroxidase (POD)) (antioxidant defense); - Downregulates gene expression of β-ketoacyl-[acyl carrier protein] synthase I (KASI) and cis-epoxy carotenoid dioxygenase 3 (NCED3) and upregulates gene expression of alternative oxidase (AOX1B), BREVIS RADIX-like homologous gene (BRXL2), WRKY transcription factor 29 (WRKY29), and EREBP transcription factor 2 (EREBP2) (gene expression and epigenetic regulation) (vs. cold-only control).	[54]

Table 1. Cont.

Stress	Plant	Type of Plasma (Parameters)	Effects on Plants and Mechanisms	Ref.
Metal toxicity	Wheat seeds (<i>Triticum aestivum</i> L.)	Low-pressure dielectric barrier discharge (5 kV, 4.5 kHz, 45 W, Ar/air gas mixture)	- Changes the seed surface and decreases pH in seeds (vs. untreated control); - Decreases root and shoot Cd concentration (vs. Cd-only control); - Upregulates SOD and CAT gene expression (antioxidant defense) (vs. Cd-only control); - Decreases TaLCT1 and TaHMA2 expression in roots (ion homeostasis) (vs. Cd-only control); - Increases total concentration of chlorophyll (growth and yield response) (vs. Cd-only control).	[55]
	Maize (<i>Zea mays</i> L.)	PAW generated by a transient spark discharge (TS, 11–13 kV, 1.5–3 kHz, 3 A; 20 mL of water exposed to plasma for 20 min)	- Improves growth of seedlings, accelerates endodermal development and root development, and results in shorter and thinner but more branched roots (vs. untreated control); - Improves maize tolerance against As stress (vs. As-only control); - Increases POX and CAT activities (antioxidant defense); - Increases pigment concentration (growth and yield response) (vs. As-only control).	[56]
	<i>B. pilosa</i> , <i>S. nigrum</i> , and <i>T. repen</i>	Atmospheric glow discharge plasma (100 W and 500 W; 60 s)	- Enhances biomass (45%), cadmium accumulation (54.4%), and Cd phytoremediation efficiency; - Affects organic acid (oxalic, tartaric, malic, acetic and citric acids) levels in roots (ion homeostasis) (vs. Cd-only control).	[57]
	Water spinach seeds (<i>Ipomoea aquatica</i>)	Atmospheric pressure plasma jet (3.0 kV, 16 kHz, 60 W, air at 10 L/min)	- Suppresses Cd absorption (22.9%) (vs. untreated control).	[58]
	Wheat (<i>Triticum aestivum</i> L.)	Cold plasma	- Alleviates Cd accumulation in roots, shoots, and grains; - Improves grain yield, particularly under severe Cd stress; - Changes physio-biochemical properties and fatty acid profile (Growth and yield response) (vs. Cd-only control).	[59]
	Soybean (<i>Glycine max</i>)	High-voltage atmospheric cold plasma (plasma-activated water (PAW), 100 mL at 30, 50, and 70 kV for 0, 3, 5, and 7 min)	- Plasma-activated water speeds up germination (maximum germination of seeds was 93.3% and 7% higher than the untreated control group) and growth; - Reduces rate of heavy-metal uptake by plants in the presence of ZnO nanoparticles.	[60]

Table 1. Cont.

Stress	Plant	Type of Plasma (Parameters)	Effects on Plants and Mechanisms	Ref.
Pathogen infection	Tomato seeds (Bacterial wilt)	Capacitively coupled plasma (CCP; 13.56 MHz, 80 W, 15 s)	- Reduces infection of tomato by bacterial wilt (caused by <i>Ralstonia solanacearum</i>) (25% vs. pathogen-only control); - Enhances seed germination rate (11%), height (10.8%), leaf thickness (10.7%), stem diameter (17.2%), dry weight (9.3%), Ca content (7.73%) and B content (11.53%) (vs. untreated control); - Increases POD, PPO and PAL activities (antioxidant defense) (vs. pathogen-only control).	[27]
	Broccoli seed	Corona discharge plasma jet (CDPJ)	- Reduces number of microorganisms on seed surface (vs. untreated control).	[32]
	Rice seedling (Bakanae disease)	Atmospheric plasma (20 kV, 10 kHz, air at 16 L min ⁻¹ , 10 cm)	- Reduces pathogenicity of bakanae disease caused by fungal pathogen <i>Fusarium fujikuroi</i> and bacterial seedling rot caused by <i>Burkholderia glumae</i>; - The bakanae disease severity index and the percentage of plants with symptoms were reduced to 18.1% and 7.8%, and the bacterial seedling blight disease index was also reduced to 38.6% (vs. pathogen-only control).	[61]
	Tomato plants (Bacterial leaf spot)	PAW generated by atmospheric pressure cold plasma (CAP; 20 kV, 1 kHz, air, treatment of 80 mL of sterile distilled water)	- Enhances defense of tomato plants against <i>Xanthomonas</i> (bacterial leaf spot of tomato); - The relative protection (RP) of PAW was 38%, and the expression of the plant defense response gene <i>pal</i> was increased (gene expression and epigenetic regulation) (vs. pathogen-only control).	[62]
	Maize (<i>Zea mays</i> L.), narrow-leaved lupine (<i>Lupinus angustifolius</i> L.) and winter wheat (<i>Triticum aestivum</i> L.)	Low-pressure plasma	- Reduces levels of seed infection (the incidence of root rot did not exceed 6.9%) and stimulates germination in the field, early growth of seedlings and resistance to pathogens during plant growth (winter wheat grain yield increased by 2.3%, that of maize by 1.7%, and that of narrow-leaved lupine by 26.8%) (26.8% vs. untreated control).	[63]
	<i>Arabidopsis thaliana</i> seedlings	Atmospheric pressure cold plasma (APCP)	- Regulates expression of adversity-responsive genes through the MAPK signal transduction pathway (regulates expression of adversity-responsive genes through the MAPK signal transduction pathway).	[64]
	Sweet basil	Cold plasma (13 kV, 28.8 kHz, helium, 5 L/min, for 5, 10, 15 min)	- Reduces incidence and severity of Fusarium wilt of basil (FOB) caused by <i>Fusarium oxysporum</i> f. sp. <i>Basilici</i> in sweet basil.	[65]

Table 1. Cont.

Stress	Plant	Type of Plasma (Parameters)	Effects on Plants and Mechanisms	Ref.
Pathogen infection	<i>Arabidopsis thaliana</i> (Cucumber mosaic virus strain yellow (CMV(Y)))	Plasma-treated gas, N ₂ O ₅ (0 s, 10 s, 20 s, 30 s, 40 s, 60 s, 2 min, or 5 min)	- Enhances <i>Arabidopsis</i> immune function by relying on the ethylene (ET) signaling pathway.	[66]
	<i>Cucumis sativus</i> , <i>Pisum sativum</i> , and <i>Vigna radiata</i>	Atmospheric pressure plasma jet (APPJ; 170 Hz, a duty cycle of 25%, helium 4.5 L/min)	- Inactivates plant pathogens <i>Dickeya solani</i> , <i>Pectobacterium atrosepticum</i> and <i>Pectobacterium carotovorum</i> ; - Reactive oxygen species (ROS) •OH, •HO ₂ , •O ₂ [−] , O ₃ , and ¹ O ₂ and reactive nitrogen species (RNS) N, NO ₂ , and NO ₃ are responsible for the antibacterial properties of APPJ; - Plant growth increase of 20.96% was observed in APPJ-exposed <i>Zea mays</i> seeds (vs. untreated control).	[67]

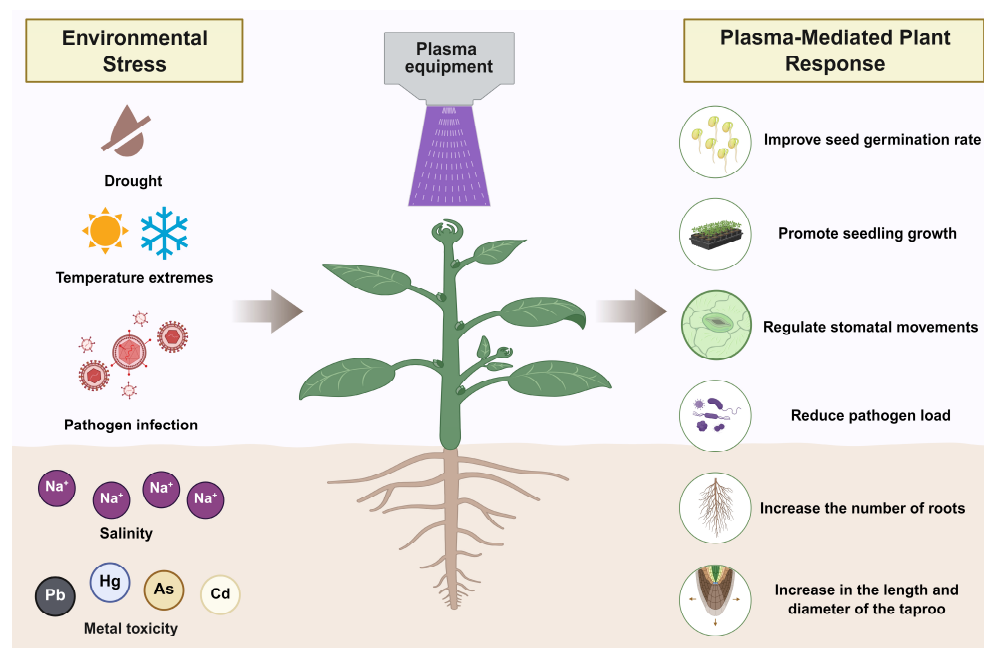


Figure 2. Summary of the role of plasma in plant resistance to environmental stress.

2.1. Drought

Drought is an environmental stress that can significantly impact the growth and development of crops on farmland. Research has shown that drought can cause various physiological changes in plants, including stomatal closure, impaired photosynthesis, changes in leaf morphology, premature senescence, and changes in the root system due to insufficient water resources [68]. Notably, plasma may mitigate the negative effects of drought on plants by increasing seed germination and seedling growth. Atmospheric dielectric barrier discharge (DBD) plasma treatment was found to promote wheat seed germination and seedling growth under drought stress [42]. Compared with the “drought stress” group, the germination rate of the “plasma + drought stress” group increased by approximately 17.3%. The germination drought resistance index also increased by 15.1%,

and the average root and shoot lengths increased by 20.0% and 31.9%, respectively [42]. Similar results were also obtained in wheat seeds treated with high-voltage electrical discharge (HVED). HVED pre-treatment can improve germination rate, germination index value, and shoot and root growth under drought conditions [43]. In addition, plasma also exhibited a promoting effect on the seed germination and seedling growth of oil seed rape, barley, alfalfa, and tomato under drought stress. The study found that capacitive coupled plasma (CCP) treatment significantly increased the germination rate of rapeseed by 6.25% and significantly increased the dry weight, root length and number of lateral roots of rapeseed [41]. Plants grown from barley seeds treated with DBD plasma under drought conditions had stronger and denser root systems than control seeds, with a 20% increase in the number of roots and 70% and 80% increases in the length and diameter of the taproot, respectively [44]. Phenotypic observations of tomato seedlings under drought stress showed that seeds primed with cold plasma had higher drought resistance potential at the seedling stage [69]. Alfalfa seeds treated with 40 W cold plasma/low-power CPT had higher germination potential, germination rate, seedling height, root length, and vigor index [70]. The mechanisms of plasma-induced drought resistance can be divided into three categories: (1) improved germination rate—plasma treatment breaks seed dormancy and enhances water absorption capacity, thereby improving germination rate; (2) improved root system—enhanced root development helps plants obtain deeper soil moisture and improve drought resistance; and (3) enhanced physiological response—plasma treatment can induce the expression of relevant genes, regulating specific physiological changes and thereby improving plant stress responses. These biological responses include antioxidant regulation, osmolyte accumulation, and ABA signaling activation.

2.2. Salinity

Salinization is known to affect plant growth by decreasing soil fertility. Studies have shown that as salinity increases, the germination rate of seeds decreases significantly. Although plasma treatment did not affect plant size and root system under salt stress, plants grown from plasma-treated seeds had higher concentrations of chlorophyll a and b, while the concentration of proline decreased by approximately 50% [44]. In addition, high-voltage electrical discharge (HVED) pre-treatment can improve wheat drought and salt resistance. Under varying levels of NaCl salt stress, HVED treatment could change the structure of wheat seed surface, making it easier to absorb water, thereby improving germination rate, germination index value, and growth of aerial parts and roots [43]. Plants grown under salt stress accumulate more Na^+ and less Ca^+ , leading to ion imbalance. Notably, APNTP treatment can alleviate this effect by reducing Na^+ accumulation and increasing K^+ and Ca^{2+} levels in plant cells under salt stress, though it cannot fully offset the impact of salt stress [47]. APNTP also upregulated the activity of enzymes related to secondary metabolic assimilation, the accumulation of reactive oxygen species (ROS), and the content of malondialdehyde (MDA) [47]. Therefore, APNTP should be considered a stress mitigation or priming tool rather than a complete solution to salinity stress.

2.3. Extreme Temperature

Temperature fluctuations can have a significant impact on seed germination and subsequent plant growth, particularly in crops that are more susceptible to temperature-related stress. Extreme temperature fluctuations have the potential to result in a reduction in crop yield or, in severe cases, complete crop failure [71]. Rice (*Oryza sativa* L.) seeds showed delayed germination under heat stress, which was associated with the expression levels of abscisic acid (ABA; a germination-inhibiting hormone) and α -amylase (starch-hydrolyzing enzyme). However, the seed germination rate was significantly restored after APNTP treat-

ment [53]. Genes involved in ABA biosynthesis (OsNCED2 and OsNCED5) were down-regulated, while genes involved in ABA catabolism (OsABA8'/OH1 and OsABA8'/OH3) and α -amylase genes (OsAmy1A, OsAmy1C, OsAmy3B, and OsAmy3E) were upregulated [53]. Similarly, the germination rate of plasma-treated seeds was higher even at low temperatures [44]. Beyond rice, APNTP treatment has also shown protective effects against temperature stress in other crops. In cotton seeds, dielectric barrier discharge (DBD) plasma treatment increased water absorption and improved germination under both warm and chilling conditions, thereby enhancing overall chilling tolerance [51]. In tomato seedlings, cold plasma treatment upregulated H₂O₂ and ABA cascade signaling, which contributed to improved cold resistance [52]. These findings suggest that ABA signaling activation may be a common mechanism by which plasma treatment enhances plant tolerance to temperature extremes across different species. This suggests that plasma appears to improve plant tolerance to extreme temperatures.

2.4. Metal Toxicity

Some contaminated soils contain a variety of toxic heavy-metal elements, which can accumulate in plants and eventually cause human poisoning [57]. In addition, these heavy metals can cause plant chlorosis, wilting, leaf curling, and slow plant growth [72]. Research has found that low-pressure dielectric barrier discharge (LPDBD) technology can alleviate the damage and growth retardation of wheat plants under cadmium (Cd) stress [55]. The mitigation effect of plasma on Cd toxicity may originate from the roots and is related to the conduction mechanism of NO [55]. Severe Cd stress leads to reduction in grain yield and monounsaturated fatty acid (MUFA) content in wheat. APNTP alleviates Cd stress by changing the physiological and biochemical characteristics and fatty acid composition of wheat, thereby optimizing wheat growth and yield [59]. In addition, plasma can play an auxiliary role in alleviating heavy-metal stress. APNTP combined with foliar-applied selenium nanoparticles can regulate Cd toxicity by changing essential oil content, chlorophyll a, chlorophyll b and total chlorophyll in sage [73]. Plasma-activated water appears to have a similar effect, as shown in soybeans (*Glycine max*), in which treatment with plasma-activated water resulted in a five-fold reduction in the uptake of heavy metals (Pb) [60]. Maize (*Zea mays* L.) treated with plasma-activated water responded to arsenic stress by improving its antioxidant capacity, mainly by increasing the contents of antioxidant enzymes (POX (peroxidases) and CAT (catalase)), non-enzyme molecules and carotenoids [56]. However, some studies have shown that the detoxification effect of plasma on heavy metals in plants may be selective. After water spinach seeds or irrigation water were treated with plasma, the bioaccumulation factor (BCF) of Cd was significantly reduced, while the BCF of Pb did not change significantly, indicating that plasma treatment may inhibit the absorption of Cd without affecting the absorption of Pb [58]. This selectivity suggests that the protective effects of plasma are metal-specific and cannot be generalized across all heavy metals. Reducing the uptake of one metal does not necessarily imply broad heavy-metal detoxification capacity. Therefore, the effectiveness of APNTP against each contaminant should be evaluated independently before large-scale application.

2.5. Pathogen Infection

There are many harmful microorganisms in nature that can cause slow plant growth. APNTP treatment reduces the incidence and severity of *Fusarium* wilt of basil caused by *Fusarium oxysporum* f. sp. *Basilici* in sweet basil [65]. Although plasma-activated water did not show direct antimicrobial activity against *Xanthomonas vesicatoria*, which causes bacterial leaf spot of tomato, it enhanced the defense capacity of tomato plants, increasing the relative protection by 61% in vitro [62]. Low-pressure plasma treatments

have demonstrated to be efficacious in the suppression of fungal crop diseases, including boil smut of maize, root rot of lupine and winter wheat [63]. This is due to reduced levels of seed infection, stimulation of germination in the field, early seedling growth, and increased resistance to pathogens during plant growth [63]. Plants treated with plasma also showed delayed disease progression and reduced disease severity. Tomatoes treated with APNTP showed a significant improvement in resistance to bacterial wilt caused by *Ralstonia solanacearum* [27]. Studies have shown that plasma treatment can lead to a significant reduction in fungal load, with untreated seeds exhibiting a pathogenicity rate of 58%, while the seeds treated with plasma demonstrated pathogenicity rates of 6.7% and 13.3%. Plasma-induced resistance was also demonstrated against bakanae disease caused by the fungal pathogen *Fusarium fujikuroi* and bacterial seedling rot caused by *Burkholderia glumae* [61]. APNTP can also be used as a method of physical disinfection for plant seeds. Microbial contamination can lead to reduced seed viability, low germination rates, and delayed germination. The study found that after two minutes of corona discharge plasma jet treatment, the number of microorganisms on the seeds, primarily aerobic bacteria, molds, and yeasts, was significantly reduced (by up to 99%) [32].

3. Plasma-Mediated Responses to Environmental Stresses in Animals

Currently, there are serious challenges to the habitats of animals and humans, such as pathogen infections, physical trauma, organic poisoning and air pollution [74] (Figure 3). These problems not only affect the health and productivity of animals but also threaten the sustainable development of society [75]. Similarly, many studies have found application prospects for plasma technology in animal fields (Tables 2 and 3). These applications can be divided into two categories. The first category includes direct biological effects on the animal, such as wound healing and reproductive enhancement. The second category includes indirect biological effects mediated by environmental interventions, such as microbial disinfection, environmental pollutant degradation, and air purification. Improving the surrounding environment can reduce the stress burden on animals. It should be noted that environmental pollutant degradation refers to the breakdown of contaminants in water, soil, and air, not metabolic processes occurring inside the animal. To elucidate the effect of plasma on animal resistance to environmental stress, we summarize and discuss the role and mechanisms of plasma technology in addressing the above-mentioned environmental and health challenges (Figures 3 and 4).

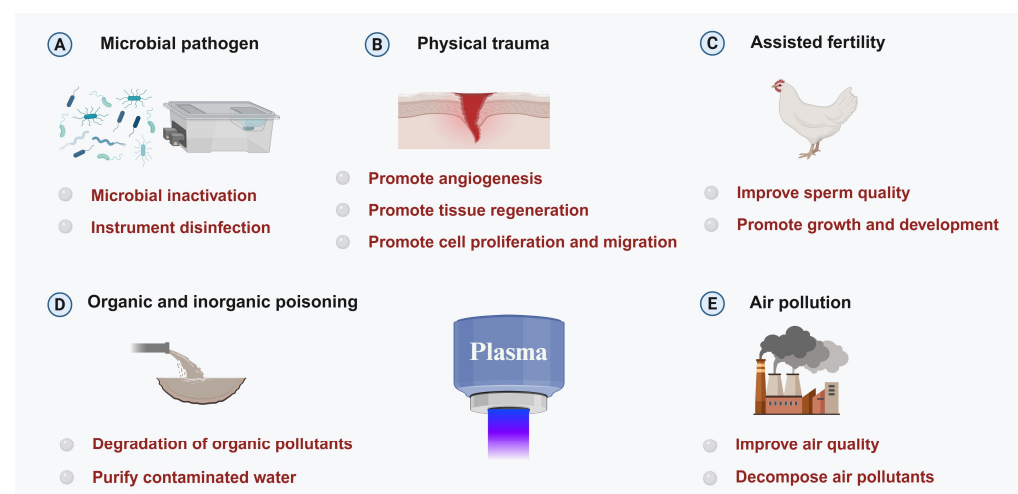


Figure 3. Summary of the role of plasma in animal resistance to environmental stress.

Table 2. Summary of tolerance to stresses and underlying mechanisms in animals induced by atmospheric pressure non-thermal plasma.

Stress	Animal	Type of Plasma	Effects on Animals and Mechanisms	Ref.
Physical trauma	Rats (scratch wound healing)	N ₂ -generated non-thermal plasma (NTP)	- Activates expression of the MMP-9/uPA system (gene expression and epigenetic regulation).	[76]
	BALB/c mice (skin wounds)	Low-temperature plasma (LTP)	- LTP treatment for 30 s elevated fibroblast proliferation and altered cell cycle progression; - Phosphorylation of P56 activates the expression of P50 protein (gene expression and epigenetic regulation); - Upregulates the expression of P-p65, downregulating the expression of IκB and activating the NF-κB signaling pathway (gene expression and epigenetic regulation) (vs. untreated control).	[77]
	Humans (nasal mucosal injury) *	Non-thermal plasma-treated solution (NTS; 3~4 kV, 25 kHz, nitrogen (N ₂) gas, 10 and 30 s, 4 cm)	- Promotes postoperative regeneration and the healing of the nasal mucosa; - Regulates the expression of EMT-related genes <i>Src</i> (p- <i>Src</i>), <i>FAK</i> (p- <i>FAK</i>), <i>AKT</i> (p- <i>AKT</i>), and <i>ERK</i> (p- <i>ERK</i>) at elevated levels (gene expression and epigenetic regulation).	[78]
	Rats (cutaneous wound)	Helium/argon cold atmospheric plasma jet (He/Ar-CAPJ; 6.5 kV, He and Ar at 5 and 0.5 L/min, 15 mm)	- Promotes granulation tissue formation and accelerates wound healing; - Stimulates p-ERK, cyclin D1 and Cdk2 EMT and cell proliferation-related gene expression (gene expression and epigenetic regulation).	[79]
	Rats (cutaneous wound)	Non-thermal plasma jet (6 kV, 12 kHz, 10 W, helium gas at 8 L/min, 1 min, 3–4 cm)	- Significantly reduces scar formation area and increases degree of epithelialization; - Accelerates wound healing (plasma treatment vs. Con, day 5: 41.27% vs. 54.7%; day 7: 56.05% vs. 75.28%; day 14: 89.85% vs. 98.07%); - Significantly downregulates scar formation-related genes TGF-β1 and p-Smad2/3 was (gene expression and epigenetic regulation) (vs. untreated control).	[80]
	Male mice (diabetic patient's wound)	Atmospheric pressure non-thermal plasma (APNTP)	- Decreases protein expression of superoxide dismutase (SOD), reducing oxidative stress levels (antioxidant defense); - Elevates protein expression of TGF-β (gene expression and epigenetic regulation); - Inhibits TGF-β1, p-Smad2, and p-Smad3 signaling pathways (gene expression and epigenetic regulation) (vs. untreated control).	[81, 82]
	New Zealand white rabbits (bone defect)	Atmospheric pressure non-thermal plasma (APNTP; 10 kV, 33 kHz, 0.47 W, helium gas at 1.5 L/min, 10 mm)	- After 10 min of NATPP treatment new bone volume was 1.51-fold greater than that in the untreated group; - Stimulates expression of cell differentiation genes MyoD and MyoG (gene expression and epigenetic regulation).	[83]

Table 2. Cont.

Stress	Animal	Type of Plasma	Effects on Animals and Mechanisms	Ref.
Physical trauma	Rats (nerve damage)	Atmospheric pressure non-thermal plasma (NTP; 3 kV, argon, 2.0 L/min, 5 min)	- NTP accelerates cell proliferation and regeneration of damaged neurons in SH-SY5Y (human neuroblastoma cells) differentiated by retinoic acid (RA); - NTP accelerates myelin sheath formation after SNCI by reducing CD68-positive macrophage accumulation (growth and yield response); - Increases expression of nerve regeneration-related genes tau, wnt3a, and β-catenin (gene expression and epigenetic regulation).	[84]
	Mice (diabetic wounds)	Atmospheric pressure non-thermal plasma jet (APPJ; 18 kV, 17 kHz, argon, 0.3 L/min)	- Levels of inflammatory cytokines, such as IL-1α, IL-1β, IL-6, and TNF-α, were significantly lower (growth and yield response) (vs. diabetic-only control).	[85]
	Humans (physical trauma) *	Cold atmospheric plasma (CAP)	- Reduces the bacterial burden at the wound site and promotes wound healing. - Enhances sustained levels of IL-1, IL-8, TGF-β, TNF-α, and INF-γ (hormonal regulation). - Improves extracellular matrix (ECM) formation through activation of canonical TGF-β1 SMAD-dependent pathway (growth and yield response).	[86]
	Mice (skin wounds)	Low-temperature cold plasma (LTCP; 0–10 kW)	- Inhibits proinflammatory factors such as TNF-α (55.98%), IL-6 (8.44%), and IL-1β (73.91%) and promotes the expression of VEGF (91.59%), bFGF (33.38%), TGF-β (39.48%), COL-1(19.86%), and SMA (8.51%) tissue repair-related factors (growth and yield response).	[87]
Fertility and reproductive health	Chicken sperm	Non-thermal dielectric barrier discharge plasma (27.6 kV, 60 Hz, argon at 2 L/min, 4 min)	- Regulates the levels of antioxidant defense-related and energetic metabolism-related genes in spermatozoa; - Decreases gene expression of NRF2 (0.6-fold), SOD (0.47-fold), CAT (0.67-fold), GPx (0.65-fold), PRDX1 (0.49-fold), PRDX3 (0.80-fold), PRDX4 (0.39-fold), and PRDX6 (0.64-fold) (gene expression and epigenetic regulation); - Increases gene expression of IGFBP2 (1.95-fold), AMPKα2 (1.15-fold), AMPKβ2 (0.74-fold), AMPKγ3 (0.68-fold), NOX4 (1.34-fold), KEAP1 (1.0-fold) and PRDX3 genes (gene expression and epigenetic regulation) (vs. untreated control).	[88]

Table 2. Cont.

Stress	Animal	Type of Plasma	Effects on Animals and Mechanisms	Ref.
Fertility and reproductive health	Chicken embryos	Non-thermal dielectric barrier discharge plasma (DBD; 11.7 kV, 16.4 kV, 22.0 kV, and 27.6 kV)	- Promotes development of chicken embryos, growth rate of chickens and reproductive capacity of roosters and facilitates poultry breeding; - Increases antioxidant enzymes SOD, CAT and GPx, and peroxiredoxins (PRDXs) (antioxidant defense); - Upregulates NRF2- and mTOR-related genes and downregulates NOX4-, KEAP1- and AMPK-related genes (gene expression and epigenetic regulation) (vs. untreated control).	[89]
	Human sperm *	Dielectric barrier discharge (DBD) plasma	Effects of sperm motility and responses to oxidative stress.	[90]
	Chicken sperm	Non-thermal dielectric barrier discharge plasma (2.81 W for 2 min)	- Improves count (0.2-fold), spermatogenesis, sperm motility (0.22-fold) and fertility (0.13-fold) of chickens; - Increases the levels of nicotinamide adenine dinucleotide hydrogen (NADH) (0.17-fold), cytochrome c oxidase (0.32-fold), and ATPase synthase (0.39-fold) and upregulates testosterone biosynthesis genes STAR, CYP11A1, CYP17A1 and HSD17B3 (hormonal regulation) (vs. untreated control).	[91]

* Human studies are included only to support a mechanistic understanding of pathways conserved across mammals.

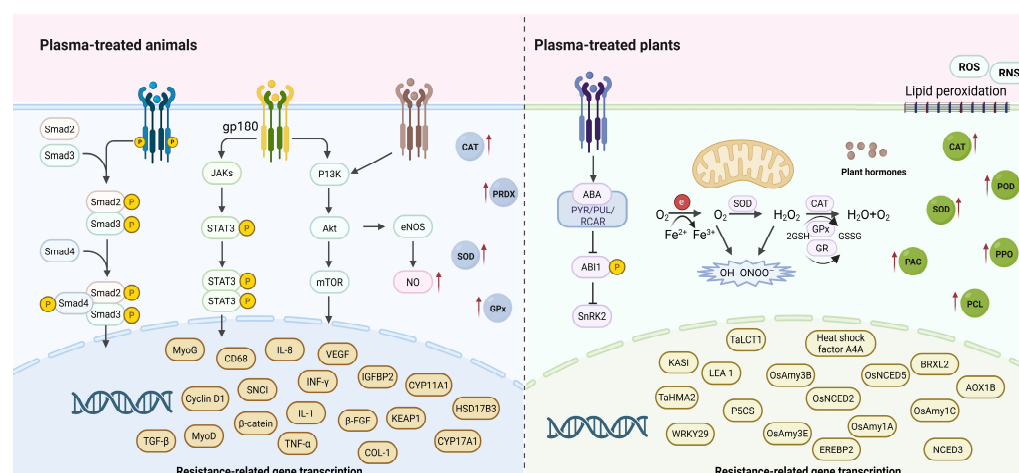


Figure 4. Schematic illustration of plasma-mediated mechanisms in plants and animals under environmental stress. Common mechanisms include the following: (i) ROS and RNS serve as universal signaling molecules, triggering downstream adaptive responses in both plant and animal cells; (ii) activation of conserved antioxidant defense systems in eukaryotes, including superoxide dismutase, catalase, peroxidase, and the glutathione system; and (iii) regulation of gene expression through conserved signaling cascades, particularly the MAPK pathway.

Table 3. Regulation of microorganisms and pollutants harmful to humans and animals by atmospheric pressure non-thermal plasma.

Stress	Stress Type	Type of Plasma	Effects of Plasma	Ref.
Harmful microbes	<i>Staphylococcus aureus</i> (MRSA), vancomycin-resistant enterococci (VRE), extended-spectrum- β -lactamase (ESBL)-producing <i>Escherichia coli</i> , and <i>Acinetobacter baumannii</i>	Cold air pressure plasma single-jet (2.5 kV, 8 kHz, 12 L/min, 0–90 s, 1 cm) and multi-jet cold plasma	- Direct plasma exposure successfully reduces bacterial load.	[92]
	<i>Pseudomonas aeruginosa</i> , <i>Escherichia coli</i> , and <i>Vibrio parahaemolyticus</i> , <i>Listeria monocytogenes</i> and <i>Staphylococcus aureus</i>	Dielectric barrier discharge cold atmospheric plasma (argon/oxygen mixture gas, 5 min)	- Cell walls of Gram-negative bacteria (GNB) are perforated, releasing intracellular compounds such as proteins and DNA, while intracellular components of Gram-positive bacteria (GPB) are oxidized and released.	[93]
	<i>Listeria monocytogenes</i> , <i>Escherichia coli</i> , <i>Pectobacterium carotovorum</i> , and sporulated <i>Bacillus atrophaeus</i>	Plasma-processed air (PPA) and plasma-treated water (PTW) (2.45 GHz, 1.1 kW, air at 18 L/min, 0–5 min)	- Plasma technology aids in disinfection and antibacterial effects in the field of food processing.	[94]
	Airborne viruses: from MS2 to coronavirus	Non-thermal plasmas (NTPs) and dielectric barrier discharge (DBD)	- ROS and RNS produced by NTP can cause conformational changes in viral capsid protein that dissociates it from the host cell, rendering it noninfectious.	[95,96]
	Herpes simplex virus type 1 (HSV-1)	Non-thermal plasma (NTP)	- NTP can regulate HSV-1 replication and solve latency problem by reducing the size of the viral reservoir in the nervous system.	[97]
Organic and inorganic poisoning	Pyrene-contaminated soil	Double dielectric barrier discharge plasma (35.8 kV, 0.85 L/min, air, nitrogen and argon)	- DDBD plasma can efficiently repair pyrene-contaminated soil and restore biological functions without changing soil physical and chemical properties; - The remediation efficiency of pyrene under air, nitrogen and argon as carrier gases were approximately 79.7, 40.7 and 38.2%; - The respiratory activity increased by more than 21 times with a pyrene remediation efficiency of 81.1%.	[98]

Table 3. Cont.

Stress	Stress Type	Type of Plasma	Effects of Plasma	Ref.
Organic and inorganic poisoning	Biotoxin patulin	Low-temperature discharge plasma (12 kV, 16 kV, and 18 kV; 30 min)	- Plasma-generated oxides can effectively break the chemical bonds of persistent pollutants (Patulin decomposition and mineralization efficiencies reached 93% and 74%); - $^1\text{O}_2$, OH, O_2^-, and hydrated electrons generated in the discharge plasma process contributed to patulin decomposition; - The lactone and hemiacetal groups that are responsible for the toxicity of patulin were significantly destroyed by discharge plasma oxidation, and some ring-opening intermediates.	[99]
	Synthetic textile dyes	Multi-electrode dielectric barrier discharge (MEDBD) plasma (15% duty cycle, 40 min)	- Synthetic textile dyes are degraded to simple forms such as CO_2, H_2O and N_2, and the degradation rate of synthetic textile dyes is greater than 95% when using plasma containing O_3 at a power of 2.44 ± 0.21 W (vs. untreated control).	[100]
	4-Nitrophenol	Argon and air-mixed argon plasma jets (5.9 kV, 31.3 kHz, 350 sccm, 0.18 W and 0.25 W)	- The Ar–air plasma jet (97.2%) treatment outperforms that of the Ar jet (75.6%); - Hydroxyl radical and ozone, along with energy from excited species and plasma-generated electron transfers, are responsible for CPJ-assisted 4-NP breakdown.	[101]
	PFAS (contaminated water in different matrices)	Non-thermal plasma at atmospheric pressure (NTP APPJ; 10 min)	- Successful removal of polyfluorinated substances (PFAS, 90%) (perfluorooctanesulfonic (PFOS, 99.89%), undecafluorohexanoic acid (PFHxA, 94.61%), dodecafluoro-3 H-4,8,-dioxanoate (ADONA, 94.83%), PFOS (50%) and hexafluoropropylene acid (GenX,32%) (vs. untreated control).	[102]

Table 3. Cont.

Stress	Stress Type	Type of Plasma	Effects of Plasma	Ref.
Organic and inorganic poisoning	Aflatoxin B ₁	Atmospheric pressure cold plasma (DBD, 5 kV, 55 kHz, 240 W/air, nitrogen, argon, and nitrogen + argon at 10 L/min, 3 cm)	- Cold plasma mitigates cytotoxicity against human hepatocellular carcinoma cells (Hep-G2) by degrading aflatoxin B1 (bioaccessibility (96.44%)).	[103]
	Waste gas streams	Atmospheric pressure non-thermal plasma	- NTP supports VOC reduction efforts.	[104]
	Built environment	Non-thermal plasma (NTP (air, 0.1–0.6 W, 0.2–2 m ³ /h, 10 min))	- Under the most suitable conditions of P = 0.6 W, Cin = 0.1 ppm, F = 0.2 m ³ /h and RH = 65%, the degree of removal of formaldehyde by NTP was as high as 99% with no subsequent pollution (vs. untreated control).	[105]
	Toluene	Catalytic non-thermal plasma (10.67–13.20 kV, 20 kHz, 44 W, 60 min)	- Toluene in air was efficiently removed by non-thermal plasma catalytic reactor; - Non-thermal plasma with TiO ₂ or Al ₂ O ₃ removed toluene at very low voltage.	[106]

3.1. Harmful Microbes

3.1.1. Farm-Environment Disinfection

Contamination of frequently touched surfaces and equipment on farms can harm animal health, leading to reduced productivity and economic losses [107]. Microorganisms present in farms can cause mastitis and endometritis in cows, as well as gastrointestinal and respiratory diseases [108]. This also includes a broader range of diseases, such as African swine fever, classical swine fever, porcine reproductive and respiratory syndrome, rinderpest, foot-and-mouth disease, and bluetongue disease, among others [109]. Therefore, sterilization and disinfection of animal farms facilitate a pathogen-free environment essential to the growth and development of animals [92,110]. APNTP effectively inactivates microbial pathogens including *Staphylococcus aureus*, *E. coli*, *vancomycin-resistant Enterococci*, *Acinetobacter baumannii*, and herpes simplex virus type 1 (HSV-1) [92,97,111]. In addition, APNTP is an effective, non-toxic, and equipment-safe sterilization method that can sterilize small items such as cages, feeding utensils, and drinking water equipment in animal farms and also effectively disinfects large surfaces such as walls, floors, and fences [95]. Studies have shown that APNTP disinfection has little effect on the quality of metals such as stainless steel, copper, tin-copper, and passive electronic components, and they can all be used normally after this process [95].

3.1.2. Wound Pathogen Reduction

Another study demonstrated that after treatment with plasma, the cell walls of Gram-negative bacteria (GNB), including *P. aeruginosa*, *E. coli*, and *Vibrio parahaemolyticus*, exhibited irreversible perforations, leading to the release of intracellular compounds such as proteins and DNA. In contrast, in Gram-positive bacteria (GPB), including *Listeria mono-*

cytogenes and *S. aureus*, intracellular components underwent oxidation and release [93]. It has been reported that APNTP disinfection technology has become an ideal choice for animal farms due to its high efficiency, lack of residue, environmental protection, and non-toxicity [94,112]. Plasma has been found to reduce bacterial burden in wounds and promote healing [86]. In conclusion, it can be demonstrated that plasma has the capacity to decontaminate wounds effectively and inactivate various pathogens, including viruses, bacteria, and fungi, thereby promoting wound healing [113,114].

3.1.3. Viral Inactivation and Vaccine Preparation

Recent studies have found that plasma can be used to generate vaccine effects, indirectly improving the resistance of animals and humans to the environment [115,116]. Plasma can destroy the proteins and genome of viruses by producing active particles (including ROS, RNS and UV photons), thereby causing them lose their pathogenicity [95,96]. It has been reported that Newcastle disease virus (NDV; LaSota) strains and H9N2 avian influenza virus (AIV; A/Chicken/Hebei/WD/98) can be completely inactivated by APNTP treatment for two minutes, and NDV vaccine can induce high-titer NDV-specific antibodies in specific-pathogen-free (SPF) chickens by APNTP treatment for two minutes [117]. In summary, APNTP, as an emerging inactivating agent, has advantages of high efficiency, safety, and stability. Vaccines treated with APNTP demonstrate potential advantages in immunogenicity and protective effects, suggesting possible future applications.

3.2. Physical Trauma

Helium/argon cold atmospheric plasma jet (He/Ar-CAPJ) treatment was found to accelerate wound healing by promoting granulation tissue formation and reducing inflammation in skin tissue in a study on wound healing in rats [79]. In addition, N₂-generated non-thermal plasma promotes wound repair by inducing epithelial–mesenchymal transition (EMT) and activating the matrix metalloproteinase-9/urokinase-type plasminogen activator (MMP-9/uPA) system in a scratch wound healing assay [76]. Similar results were obtained when investigating the therapeutic effects of a non-thermal microplasma jet device array on second-degree burns in a rat model, where plasma reduced the trauma area and was able to modulate inflammatory gene expression, again contributing to epithelial tissue regeneration [118]. Studies showed that APNTP promoted neuron regeneration in rats [84]. In a study of the effects of APNTP on functional recovery after sciatic nerve damage (ND), it was found that APNTP treatment could restore the level of the sciatic nerve by 60% [78]. In addition, after seven days following the treatment of Sprague–Dawley (SD) rats with muscle defects using APNTP, a significant increase in the number of satellite cells was observed compared with the untreated group, demonstrating that APNTP also has a beneficial effect on muscle repair after injury [83].

Plasma is also considered a novel approach in fracture treatment. White rabbits showed ideal bone regeneration after 10 min of APNTP treatment, and that the volume of new bone in the plasma-treated group was 1.51-fold greater than in the untreated group [83]. Plasma has also been demonstrated to inhibit scar formation following injury. Plasma jet treatment of injured mice demonstrated that the scar area of plasma-treated rats was observably smaller than that of the plasma-untreated group at 21 postoperative days, and the degree of epithelialization of the scars was significantly higher than that of the untreated group [80]. In addition, plasma treatment of rat wounds accelerates wound healing, reduces scar area and inhibits the formation of scar signaling pathways such as TGF- β 1, p-Smad2 and p-Smad3 [82]. Overall, plasma has a beneficial effect on wound healing, tissue regeneration, cell proliferation, cell migration and angiogenesis. It should be noted that the evidence presented is primarily derived from experimental animal models

(mice). Analysis of these findings contributes to understanding the conserved wound healing mechanisms across mammals. However, direct extrapolation to livestock and production animals still requires further species-specific validation.

3.3. *Insufficient Fertility and Reproduction*

APNTP technology can be used as a new technology to help solve some problems in animal fertility. Current studies have shown that APNTP technology can be used to promote the growth of rooster embryos [88]. The sperm quality-promoting effect of plasma treatment was regulated by the significant improvements in adenosine triphosphate production and testosterone level and by the modulation of reactive oxygen species balance and adenosine monophosphate-activated protein kinase and mammalian target of rapamycin pathway in the spermatozoa [91]. According to previous study, APNTP affects the fertility of animals by mediating ROS balance, energy metabolism and antibacterial effects [89,119]. APNTP can induce intracellular ROS production, and the balance between ROS production and clearance activity is necessary to ensure optimal sperm quality. A certain amount of ROS can stimulate sperm energy acquisition, the acrosome reaction, and chemotactic and oocyte fusion. The effect of plasma may be dose-dependent, and plasma can promote growth and development under appropriate conditions. However, plasma has a narrow beneficial range. Excessive exposure may negatively impact sperm viability, motility, or embryo development. Therefore, precise control of plasma parameters is critical to ensuring beneficial biological outcomes.

3.4. *Organic and Inorganic Poisoning (Pesticide Residues, Antibiotics, and Mycotoxins)*

There is a wide variety of pollutants in the environment, mainly in water, food and soil, including pesticide residues, antibiotics, microplastics and mycotoxins, among others. Most of these pollutants have a variety of toxic effects, such as organ toxicity, neurotoxicity, developmental and reproductive toxicity, and immunotoxicity, posing serious threats to animal health. For example, patulin is a neurotoxic secondary metabolite with strong toxicity to animal tissues and cells and has been reported to cause renal congestion, pulmonary edema, peritoneal and pleural effusion, and tissue necrosis in mice [99]. Chemical residues (e.g., organic dyes, fertilizers, and pesticides) that can be toxic, mutagenic, and carcinogenic to humans, have been linked to a wide range of diseases, such as cancers, hormonal disorders, asthma, allergies, reproductive disorders, neurological disorders, skin disorders, visual disturbances, and immune system-related disorders.

Given these threats, APNTP has received much attention as an effective strategy for the detoxification and removal of environmental pollutants in water [99,100]. In aquatic environments, APNTP can effectively degrade pesticide residues such as polycyclic aromatic hydrocarbons (PAHs) and polychlorinated biphenyls (PCBs) by destroying the chemical structure of organic pollutants through oxidation by ROS and reactive nitrogen species (RNS) [98]. In plasma reactions, introduction of ambient air into an argon–air plasma jet generates an abundant source of ROS and RNS, including hydroxyl radicals (OH), singlet oxygen ($^1\text{O}_2$), nitric oxide (NO), nitrate (NO_3), dinitrogen trioxide (N_2O_3), and dinitrogen pentoxide (N_2O_5). Consequently, argon–air plasma injection emerged as a promising catalyst-free solution for 4-nitrophenol (4-NP) degradation in wastewater with higher ROS and RNS generation without the need for a catalyst [101]. Low-temperature plasma treatment can also significantly reduce pesticide (dichlorvos, malathion and endosulfan) content in water [120]. These degradation reactions are mainly caused by ROS and RNS in the plasma. Beyond water treatment, plasma technology has also demonstrated considerable potential in protecting animal health through the detoxification of contaminated feed. Studies have found that plasma treatment can significantly reduce deoxynivalenol

(DON) contamination in feed substrates [121]. Furthermore, plasma-activated water (PAW) has been shown to effectively degrade multiple mycotoxins in feed, including aflatoxin B1, ochratoxin A, and fumonisin B1 [122]. Collectively, these findings highlight the broad applicability of APNTP-driven ROS/RNS oxidation in mitigating diverse environmental and feed-borne contaminants that threaten animal health.

3.5. Air Pollution

Currently, with the rapid development of industries, chemical fuels and various air pollutants are being emitted into the air in large quantities, and this has led to an increase in airborne particulate matter. This increase in airborne particulate matter can lead to a range of respiratory diseases in humans and animals, such as asthma, lung cancer, acute respiratory infections, and chronic bronchitis [123]. Many types of particulate matter can be easily inhaled and adhere to the respiratory tract, trachea, bronchus and even alveoli. The products of the reaction of NO and SO₂ with the generated aerosol particles of NaClO₂, NO₂ gas, and aqueous ions such as NO²⁻, NO³⁻, HSO³⁻, and SO₄²⁻ lead to inflammation, oxidative stress, and fibrosis [124]. Studies have found that plasma technology not only has the potential to improve air quality and reduce air pollution but also has the advantage of being more energy-efficient than other technologies [104]. In the food industry, plasma has been reported to improve air quality and eliminate volatile organic compounds. The high-energy electron bombardment in APNTP can change ground-state molecules to their sub-stable or excited states, and the products undergo multi-level physical and chemical reactions to form ions and free radicals, which react with gaseous pollutants and intermediates produced by electron collisions with precursors to ultimately produce harmless products [104]. APNTP can also break down formaldehyde (HCHO), a typical volatile organic compound in indoor air, and convert it into CO₂ and H₂O [105]. Beyond indoor environments, APNTP technology has also demonstrated considerable potential to improve air quality within livestock barn environments, where ammonia accumulation and volatile organic compounds pose significant threats to animal health. Ferroelectric plasma reactors have demonstrated significant efficacy for ammonia and odor removal in swine facilities [125], and plasma treatment in pig houses has achieved a 63.87% reduction in NH₃ [126]. Moreover, APNTP is more energy-efficient than other technologies and can remove multiple air pollutants simultaneously [127].

4. Regulatory Mechanisms of Plasma-Mediated Promotion of Tolerance to Environmental Stresses

4.1. Plasma-Mediated Stress Tolerance Mechanisms in Plants

Recent mechanistic studies have elucidated that plasma treatment confers multi-stress tolerance through diverse molecular and biochemical mechanisms. At the epigenetic level, plasma induces DNA demethylation of abscisic acid catabolism genes and α -amylase (starch-hydrolyzing enzyme) genes, thereby reversing heat stress-induced germination inhibition [53]. Under low-temperature stress, plasma activates phosphotransferase activity, modulates phosphorus compound metabolism, and triggers defense responses that maintain cellular homeostasis [54]. Plasma exposure also significantly enhances the activities of catalase (CAT) and ascorbate peroxidase (APX), which scavenge excessive reactive oxygen species and confer drought stress tolerance [45]. Furthermore, non-thermal plasma treatment upregulates CAT and superoxide dismutase (SOD) activities while inducing stress-responsive genes (including chitinase and xylanase inhibitor protein genes), thereby enhancing seed tolerance to salt-alkali stress [48]. Notably, plasma exhibits dual functionality by simultaneously promoting plant stress tolerance and exerting antimicrobial effects. The antimicrobial properties are mediated by plasma-generated reactive oxygen species

(ROS) and reactive nitrogen species (RNS), including hydroxyl radicals ($\bullet\text{OH}$), peroxy radicals ($\bullet\text{HO}_2$), superoxide anions ($\bullet\text{O}_2^-$), ozone (O_3), singlet oxygen ($^1\text{O}_2$), nitric oxide (NO), nitrogen dioxide (NO_2), and nitrate (NO_3^-), which disrupt microbial membrane integrity and cellular functions [67].

4.2. Plasma-Mediated Regulatory Mechanisms in Animals and Environmental Remediation

4.2.1. Wound Healing Mechanisms

In summary, accumulating evidence demonstrates that plasma accelerates wound healing through coordinated regulation of multiple molecular mediators. Plasma modulates the expression of IL-6, IL-8, MCP-1, TGF- β 1, and TGF- β 2 and promotes the production of collagen type I and alpha-SMA [128]. The wound healing process involves activation of critical signaling pathways, including yes-associated protein/transcriptional coactivator with PDZ-binding motif (YAP/TAZ), β -catenin, and TGF- β [129]. These molecular cascades accelerate lipid metabolism, facilitate fibrin deposition, and enhance granulation tissue formation, neovascularization, and re-epithelialization [130]. Furthermore, plasma exhibits potent antimicrobial properties by significantly reducing wound bacterial burden. This antimicrobial effect is mediated through Rac-GTP-dependent activation of NADPH oxidase 2 (NOX2), which generates superoxide anions that eliminate pathogens [131].

4.2.2. Reproductive Mechanisms

In the context of fertility and reproduction challenges, plasma treatment significantly improves sperm quality through multiple mechanisms. Plasma-treated sperm display increased progressive motility and viability, decreased reactive oxygen species (ROS) levels, and upregulated expression of key proteins including kelch-like ECH-associated protein 1 (KEAP1), nuclear factor erythroid 2-related factor 2 (NRF2), NAD(P)H quinone dehydrogenase 1 (NQO1) and glutathione peroxidase 8 (GPx8) [132]. Mechanistically, DBD plasma modulates sperm ROS homeostasis through miRNA-mediated regulation of the KEAP1/NRF2 signaling pathway [132]. Furthermore, DBD plasma increases exon methylation levels of the AMP-activated protein kinase (AMPK) gene, thereby improving glycolytic flux, mitochondrial function, and antioxidant capacity. Importantly, these beneficial effects are achieved without compromising sperm DNA integrity or acrosome structure, ensuring reproductive viability [119].

4.2.3. Environment Pollutant Degradation Mechanisms

Plasma-mediated degradation of organic and inorganic pollutants is primarily based on advanced oxidation processes (AOPs). Plasma-generated reactive oxygen and nitrogen species (RONS) ultimately reach water or gas phases containing antimicrobial agents and organic contaminants. RONS with the highest oxidation potentials preferentially attack pollutants, triggering oxidation, mineralization, and molecular backbone fragmentation or addition–elimination reactions at specific functional groups or atoms [133,134]. Beyond RONS, plasma generates solvated electrons, ultraviolet radiation, thermal energy, and electromagnetic fields. These synergistic factors trigger cascade reactions that continuously degrade organic compounds, ultimately achieving degradation and inactivation of multiple hazardous substances in liquid or solid matrices [134].

4.3. Common Plasma-Activated Regulatory Mechanisms in Plants and Animals

4.3.1. Plasma-Activated Signaling Pathways

The transforming growth factor- β (TGF- β 1)/small mothers against decapentaplegic (Smad)2/3 pathway is one of the important signaling pathways in scar formation. Following plasma treatment, the TGF- β /Smad2/3 pathway upregulates extracellular matrix remodeling genes, including collagen type I (COL1A1), fibronectin, and α -smooth

muscle actin (α -SMA), all of which orchestrate tissue regeneration and wound healing processes [80]. Vascular endothelial growth factor A/vascular endothelial growth factor receptor 2 (VEGFA/VEGFR2) is an angiogenesis-related signaling pathway. Atmospheric pressure cold plasma (APCP) induces phosphorylation and activation of endothelial NO synthase (eNOS). This activity increases the level of endogenous NO in endothelial cells, which in turn stimulates VEGFA/VEGFR2 signaling to regulate angiogenesis in vitro [82]. Wingless/Int (Wnt) is a family of signaling proteins involved in various developmental functions. Expression levels of Wnt-related genes that promote cell proliferation in the neural tube after NTP treatment were significantly increased, confirming that NTP-treated retinoic acid (RA)-differentiated SH-SY5Y (human neuroblastoma cells) cells can stimulate Wnt signaling to promote nerve regeneration [84]. The (phosphatidylinositol 3-Kinase/protein kinase B/mammalian target of rapamycin) PI3K/AKT/mTOR signaling pathway is critical to cell proliferation. Treating HaCaT cells with low doses of NTP was found to promote cell proliferation by activating the PI3K/AKT/mTOR signaling pathway, and the increased expression of signal transducer and activator of transcription 3 (STAT3) and Cyclin D1 was observed [135]. Non-thermal plasma-treated solution (NTS) acts on BEAS-2B (human bronchial epithelial cell line cells similar to nasal mucosal epithelium) and is found to stimulate epithelial–mesenchymal transition (EMT) signaling pathways to induce cell migration to promote skin wound healing [78].

In plants, atmospheric pressure cold plasma (APCP) treatment of early *Arabidopsis* seedlings can regulate the expression of adversity-responsive genes through the mitogen-activated protein kinase (MAPK) signal transduction pathway, thereby promoting *Arabidopsis* seedling growth [64]. Plasma can also downregulate the expression of viral genes angiotensin-converting enzyme 2 (ACE-2), spike (S) gene, and RNA-dependent RNA polymerase (Rd/Rp) helicase gene, as well as the protein expression of interleukin-6 (IL-6), tumor necrosis factor- α (TNF- α), interleukin-1 β (IL-1 β), interferon- γ (IFN- γ), cyclooxygenase-2 (COX-2), C-X-C motif chemokine ligand 10 (CXCL-10), and C-C motif chemokine ligand 5 (CCL-5) through the NF- κ B and MAPK pathways [136]. H₂O₂ and abscisic acid (ABA) are signaling pathways associated with cold stress resistance. The application of cold plasma (CP) as a seed treatment has been demonstrated to induce the upregulation of H₂O₂ and ABA cascade signaling, which in turn upregulates the cold-acclimated inducer of c-repeat binding factor expression 1 (ICE1) and c-repeat binding factor (CBF) genes, thereby enhancing the cold resistance of tomato plants [52]. Elevated levels of H₂O₂ and NO present in cold atmospheric plasma activation have the capacity to induce the MAPK signaling pathway, thereby stimulating the expression of pathogenesis-related (PR) proteins, antioxidant enzyme activity, and defense hormone (salicylic acid and jasmonic acid) pathway enzymes. When *Arabidopsis* plants infected with cucumber mosaic virus strain yellow (CMV(Y)) were exposed to nitrogen pentoxide (N₂O₅) generated by plasma treatment, the resistance of *Arabidopsis* to CMV was enhanced, and N₂O₅ could enhance *Arabidopsis* immune function by relying on the ethylene (ET) signaling pathway [66].

4.3.2. Plasma Activation of Related Genes in Response to Environmental Stress

APNTP can make cells exhibit unusual physiological states by activating important regulatory genes in cells [137]. This characteristic provides a new direction for APNTP-mediated resistance of external environmental stimuli [138]. Low-temperature cold plasma treatment of wounds inhibits generation of proinflammatory factors such as TNF- α (tumor necrosis factor-alpha), IL-6 (interleukin-6), and IL-1 β (interleukin-1 beta) and promotes the expression of VEGF (vascular endothelial growth factor), bFGF (Basic Fibroblast Growth Factor), and TGF- β (transforming growth factor-beta) in tissue [87]. After fibroblasts are treated with low-temperature plasma, P56 can be phosphorylated, and the expression

of proteins such as P50 can be activated to promote the recovery of fibroblasts at the wound [77]. In animals, APNTP treatment under appropriate conditions can promote the expression of growth-related factors such as thyroid hormones and growth hormones and promote growth efficiency in animals [34]. Some products of photosynthesis also play a key role in plant immunomodulation [139]. In terms of genes regarding plant dehydration resistance, it was found that the expression of SnRK2-related genes of ABA (abscisic acid) was upregulated, thereby improving the drought resistance of plants [42].

4.3.3. Plasma-Enhanced Antioxidant Defense System

Antioxidant enzymes are organic molecules that maintain cellular redox balance in organisms. Treatment of wounds in diabetic patients with APNTP showed a significant decrease in protein expression of superoxide dismutase (SOD), reducing oxidative stress levels [82]. Chicken sperm obtained low levels of ROS and malondialdehyde (MDA) after exposure to APNTP, and the increased activity of SOD, catalase (CAT), and glutathione peroxidase (GPx) enhanced antioxidant defense, improving chicken sperm mobility [89]. The same study showed that the concentration of SOD, CAT, and GPx in chicken serum after plasma treatment significantly increased, which promoted the growth and development of chickens [34].

Similar results were obtained in plants after plasma treatment. Signal molecules produced by plasma, especially ozone, nitric oxide and/or ultraviolet radiation, induced an increase in peroxidase and phenylalanine ammonia lyase (PAL) activities [140]. DBD plasma treatment significantly improves the SOD, catalase (POD) and CAT activities of wheat seedlings under drought stress, accelerating the removal of ROS, thereby reducing oxidative damage and helping to maintain normal physiological metabolic activity [42]. Similar studies found that low-temperature plasma treatment enhances the SOD and CAT activities of rapeseed seedlings under drought stress and improves their growth [41].

Ar/air plasma treatment helped detoxifying cadmium (Cd) in wheat, where plasma alleviated Cd-induced H₂O₂ rise and oxidative damage in tissues by inducing upregulation of antioxidant enzymes (SOD and CAT) and their corresponding genes (TaSOD and TaCAT) [55]. Cold plasma reduces bacterial blight symptoms caused by *R. solanacearum* in tomatoes by enhancing the activity of POD, polyphenol oxidase (PPO) and PAL [27]. In summary, plasma treatment can improve wound healing and development in animals by reducing the oxidative stress level and alleviate hindered growth and development in plants caused by oxidative stress. Importantly, ROS/RNS play a dual role in biological systems. At moderate levels, they function as important signaling molecules that regulate processes such as growth, stress adaptation, and defense responses. However, when ROS/RNS are excessively generated or not properly controlled, they can overwhelm the antioxidant defense system and cause oxidative damage to lipids, proteins, and DNA.

4.3.4. Plasma Reduces the Threat of Harmful Microorganisms to Plants and Animals

Studies have shown that plasma therapy can effectively inhibit the activity and pathogenicity of microorganisms. The use of cold atmospheric surface microdischarge plasma devices can effectively inactivate bacteria and yeast pathogens in the air [141]. Various treatments using non-thermal plasma can lead to morphological changes in the mycelium structure of plant pathogenic fungi (*F. oxysporum*, *B. cinerea*, and *A. alternata*) and severely reduce pathogenicity [142]. ROS, RNS and acid produced by plasma can completely react with polysaccharides, lipids, proteins and nucleic acid molecules in biofilms, thereby destroying the cell membrane and inactivating microorganisms [143,144]. Furthermore, studies have shown that UV light in plasma affects the upper layer of the biofilm matrix, allowing ROS and RNS to enter. It can also destroy protein content in the outer membrane by weakening chemical bonds [144]. In a similar manner, hydrogen peroxide,

produced in plasma-activated water (PAW), can undergo a secondary reaction with iron substances and the downstream products of this reaction cause DNA damage, which in turn can lead to mutations in biofilm-producing cells [145].

In addition, ROS and RNS generated by plasma can directly interact with specific intracellular molecules, thereby participating in a variety of physiological processes. In plant cells, H_2O_2 function as signaling molecules that activate calcium channels in guard cells, triggering stomatal closure under drought stress. This H_2O_2 -mediated calcium influx represents a critical early response in ABA-dependent stress signaling pathways [146]. plasma-derived NO acts as a mobile signaling molecule that can diffuse across membranes and modify cysteine residues in target proteins through S-nitrosylation, thereby modulating protein function and stress response pathways [147].

In bacterial cells, ROS and RNS cause oxidative damage to membrane phospholipids through lipid peroxidation, resulting in increased membrane permeability and leakage of intracellular contents. For Gram-negative bacteria, this oxidative attack creates irreversible perforations in the cell wall, leading to release of proteins and DNA, while in Gram-positive bacteria, the reactive species penetrate the thicker peptidoglycan layer to oxidize intracellular components directly [144]. ROS also interact with nucleic acids by inducing strand breaks and base modifications in DNA [148].

In mammalian wound healing, plasma-generated ROS stimulate the phosphorylation of endothelial nitric oxide synthase (eNOS), which increases endogenous NO production. These ROS also enhance the expression of pro-angiogenic factors including platelet-derived growth factor receptor (PDGFR) and cluster of differentiation (CD31). Together, these effects activate the VEGFA/VEGFR2 signaling pathway to promote angiogenesis [149]. The dose-dependent nature of these interactions is critical, as moderate ROS levels activate protective antioxidant enzyme systems (SOD, CAT, and POD) and stress-responsive genes, while excessive ROS accumulation leads to cellular damage through protein carbonylation and membrane disruption [150].

5. Limitations, Challenges, and Adverse Effects of Plasma Applications

While APNTP technology shows considerable promise, several limitations and potential adverse effects must be acknowledged (Figure 5). First, excessive ROS and RNS production can lead to oxidative damage, including lipid peroxidation, protein denaturation, and DNA strand breaks, particularly when treatment parameters are not optimized. Studies have reported that prolonged or high-intensity plasma exposure may inhibit seed germination, reduce cell viability, and even induce mutagenic effects in certain plant and animal models [151]. Second, the biological responses to APNTP are highly dose-dependent and species-specific, resulting in significant variability and occasional contradictory findings across experiments [152].

In addition, a critical barrier to widespread adoption and clinical/agricultural translation of APNTP technology is the lack of standardization in treatment protocols [153]. It is worth noting that a universal “recipe” for plasma treatment is unlikely to be achievable, given the large biological diversity across species, cultivars, and developmental stages. Therefore, the goal of standardization should not be to establish a single set of parameters applicable to all organisms, but rather to develop species-specific and stage-specific protocols. To illustrate the current state of parameter reporting, Table 4 summarizes the ranges of key treatment parameters (voltage, gas composition, and exposure time) documented in existing studies for the same species. This allows readers to identify optimized parameters for specific target organisms and provides a reference framework for future protocol development. Moreover, different plasma generation devices produce dramatically different outputs. Dielectric barrier discharge, plasma jets, corona discharge, and

microwave plasma systems generate distinct profiles of reactive species, electron densities, gas temperatures, and spatial distributions [154]. Even when targeting the same biological tissue under seemingly identical conditions, device-specific characteristics can lead to fundamentally different biological outcomes (Table 4). And the choice of working gas fundamentally determines plasma chemistry and biological effects. Inert gases like argon and helium generate high concentrations of metastable excited particles and UV photons, and nitrogen-containing gases such as air and N₂ produce abundant reactive nitrogen species (RNS: NO, NO₂, N₂O₅, and ONOO[−]) [155–157]. Moreover, treatment parameters including voltage, frequency, pulse width, duty cycle, exposure time, target distance, and gas flow rate collectively determine the effective “dose”. These dose–response relationships are highly species-specific and context-dependent [156].

Table 4. Comparative efficacy of different plasma types across applications in plants and animals.

Stress	Type of Plasma	Plasma Control Factor	Outcome	Parameters of Control Factor	Efficacy	Ref.
Organic and inorganic poisoning	DBD reactor (air, 10 min)	Power	HCHO removal efficiency	0.1 W	45%	[105]
				0.2 W	66%	
				0.3 W	72%	
				0.4 W	88%	
				0.5 W	90%	
		0.6 W		97%		
		1.5 m ³ /h		45%		
		0.8 m ³ /h		64%		
		0.6 m ³ /h		73.1%		
		0.4 m ³ /h		81.3%		
	0.2 m ³ /h	83.7%				
	DBD configuration reactor (13.20 kV, 20 kHz, 44 W, 60 min)	Gas flow rate	Removal of HCHO in air	30 NL/h	96%	[106]
				20 NL/h	97%	
10 NL/h				97%		
	Gas composition	Bioaccessibility of aflatoxin B1	Air	5.22%	[103]	
			Nitrogen	38.17%		
			Argon	54.38%		
			Nitrogen + argon	21.48%		
Fertility and reproductive health	Non-thermal DBD plasma (20 s)	Voltage	Sperm viability	11.7 kV	85.11%	[34]
				16.4 kV	77.33%	
				22.0 kV	71.65%	
				27.6 kV	65.84%	
			Sperm motility	11.7 kV	45.42%	
				16.4 kV	35.92%	
				22.0 kV	31.55%	
				27.6 kV	24.38%	

Table 4. Cont.

Stress	Type of Plasma	Plasma Control Factor	Outcome	Parameters of Control Factor	Efficacy	Ref.
Fertility and reproductive health	Non-thermal DBD plasma (11.7 kV)	Treatment time	Sperm viability	10 s	85.06%	[34]
				20 s	85.11%	
				40 s	84.16%	
				60 s	76.26%	
				80 s	66.23%	
			Sperm motility	10 s	42.17%	
				20 s	45.42%	
				40 s	42.36%	
				60 s	30.67%	
				80 s	25.58%	
Salt stress	DBD instrument (10 V, air)	Treatment time	0 mM NaCl	6 min	25%	[50]
				8 min	56%	
				10 min	45%	
			100 mM NaCl	6 min	23%	
				8 min	56%	
				10 min	18%	
			200 mM NaCl	6 min	14%	
				8 min	47%	
				10 min	11%	
			100 mM NaCl	6 min	22%	
				8 min	37%	
				6 min	38%	
			200 mM NaCl	8 min	50%	
				6 min	20%	
				8 min	40%	
			100 mM NaCl	6 min	35%	
				8 min	50%	
Salt stress	CCP-NTP reactor (250 V, 13.56 MHz, air)	Treatment time	Improvement in acid detergent fiber degradability	1 min	65.63%	[49]
				2 min	60.89%	
Physical trauma	Microplasma jet (10 kV, 33 kHz, 0.47 W, helium gas at 1.5 L/min, 10 mm)	Treatment time	Average occupancy of the defect site	5 min	67%	[83]
				10 min	83%	
				15 min	70%	

Table 4. Cont.

Stress	Type of Plasma	Plasma Control Factor	Outcome	Parameters of Control Factor	Efficacy	Ref.
<i>F. oxysporum</i> infection	DBD plasma (5.5 kV, 38 kHz, 9 W, Air)	Number of plasma treatments	Decrease in disease incidence percentage	5 treatments	40.0%	[142]
				10 treatments	33.8%	
				15 treatments	21.0%	
5 treatments				44.6%		
10 treatments				43.2%		
15 treatments				25.6%		
<i>A. alternata</i> infection				5 treatments	44.4%	
				10 treatments	33.2%	
				15 treatments	25.6%	

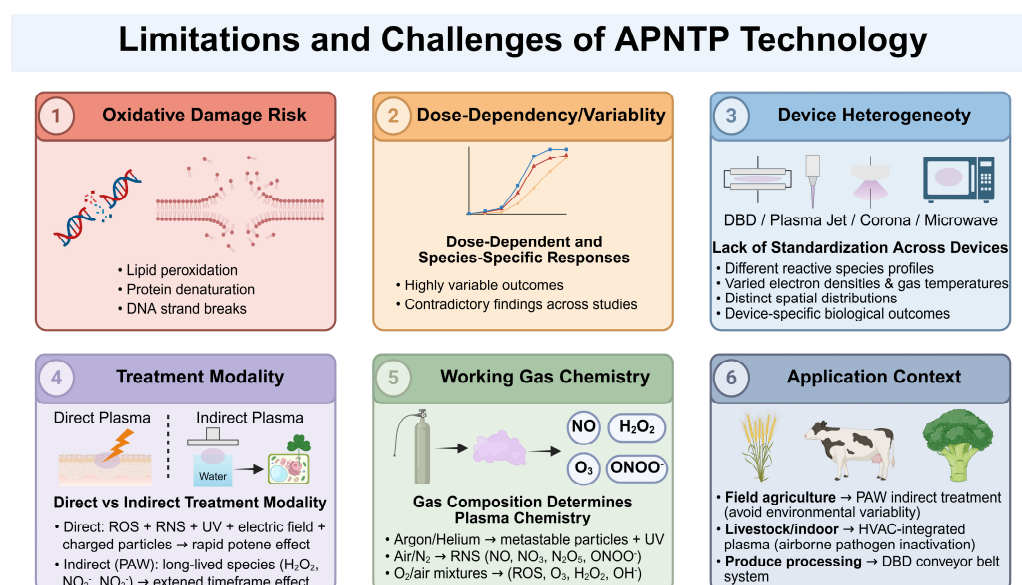


Figure 5. Summary of key limitations and challenges in the application of plasma technology.

Finally, the treatment modality further determines biological outcomes. Direct plasma exposure delivers a complex mixture of reactive species, UV radiation, electric fields, and charged particles in a single step, resulting in rapid and potent biological effects. By contrast, indirect methods using plasma-activated water or treated gases depend on long-lived chemical species (e.g., H_2O_2 , NO_2^- , and NO_3^-) that persist in the medium and act over extended timeframes [157]. To advance practical implementation of plasma technology, we advocate for the adoption of unified dosimetry metrics including energy dose per unit area (J/cm^2), concentrations of key reactive species (H_2O_2 , NO_2^- , and O_3), and UV flux measurements. Systematic dose–response studies should be conducted for each specific application scenario, target organism, and stress type. We also recommend establishing open-access databases documenting plasma treatment parameters alongside biological

outcomes. These efforts will facilitate standardization and may help lay the groundwork for the eventual translation of APNTP technology from laboratory to field applications.

Although most APNTP agricultural research remains at the laboratory scale, many studies have demonstrated translational potential for practical applications. Due to environmental variability and equipment constraints, outdoor field application presents considerable challenges. Consequently, most field-oriented studies have adopted plasma-activated water (PAW) as an indirect treatment approach. PAW not only delivers biological effects comparable to direct plasma treatment but also avoids the influence of environmental factors. For livestock applications, indoor treatment is more suitable. APNTP effectively inactivates airborne bacteria and fungi and can be integrated into existing heating, ventilation, and air conditioning (HVAC) systems [107]. For agricultural produce processing, DBD-based systems have been validated for treating fresh produce on conveyor belts [158]. In terms of energy efficiency, DBD is the most energy-efficient, followed by plasma jets, whereas corona and glow discharge consume the highest energy [23].

Most existing studies only evaluate first-generation (F1) responses to plasma treatment, and data on multi-generational genetic effects remain very limited. Previous studies have discussed the potential for epigenetic effects, DNA damage, and chromosomal aberrations following non-thermal plasma exposure and have called for systematic multi-generational safety assessments [159]. A study demonstrated epigenetic DNA methylation changes in rice after plasma treatment, suggesting that plasma exposure can induce heritable epigenetic modifications [160]. Therefore, multi-generational safety assessment following plasma treatment is a prerequisite for large-scale field application.

6. Conclusions and Future Perspectives

As an emerging technology, APNTP has shown wide application prospects in agriculture and animal health. Research shows that APNTP has a significant promoting effect on plant growth, stress resistance and animal health maintenance, and its action mechanisms show certain commonalities in animals and plants. In the field of agriculture, plasma treatment can significantly increase plant resistance to extreme weather, soil pollution and biological stress. Plasma can promote plant vegetative growth, root development and seed germination by activating specific signaling pathways and gene expression. In addition, plasma-treated plants exhibit stronger antioxidant capacity, primarily by enhancing the expression of antioxidant enzymes. APNTP also shows many advantages in animal health. It can effectively eliminate microorganisms in the animal feeding environment, reduce the use of chemical reagents, remove environmental pollution, promote wound healing and reduce animal deaths caused by accidental trauma. APNTP treatment also reduces the ammonia produced during animal feeding and the risk of respiratory diseases in animals and improves animal welfare. It should also be noted that plasma can increase animal sperm activity, which is of great significance in dealing with the problem of declining animal fertility. As a technology with wide application prospects, APNTP has great potential in fighting environmental stress. This review provides a theoretical basis for the future application of plasma technology in different fields.

Despite these promising results, several critical challenges must be addressed before APNTP can transition from laboratory research to widespread field applications. The foremost challenge is the lack of standardization in treatment parameters across studies. Variations in plasma source types, gas composition, treatment duration, and energy input hinder the establishment of reproducible protocols and complicate cross-study comparisons. In addition, the biological effects of plasma are fundamentally mediated by reactive oxygen and nitrogen species, which operate within a narrow therapeutic window. Excessive RONS production can induce oxidative stress beyond cellular antioxidant capacity, resulting in

lipid peroxidation, protein carbonylation, and damage to nucleic acids. Several studies have reported DNA strand breaks and chromosomal aberrations following high-intensity or prolonged plasma exposure, raising concerns about potential mutagenic effects. In agricultural applications, unintended genetic alterations in crop germplasm could compromise breeding programs and food safety. In animal health contexts, germline mutations could have transgenerational consequences. Moreover, the scarcity of cost–benefit analyses in the current literature makes it challenging to evaluate the economic competitiveness of plasma technology compared with conventional approaches. Although plasma treatment can reduce pesticide dependence, whether the associated equipment costs and energy consumption outweigh the savings from decreased chemical inputs remains uncertain, especially in small-scale agricultural contexts. Furthermore, the data for plasma under field and farm conditions are also limited. The actual effects under complex environmental and biological conditions remain unclear. Therefore, safety, biological effects, and cost-effectiveness must be carefully evaluated before plasma large-scale promotion.

From a mechanistic perspective, future investigations should employ multi-omics approaches integrating transcriptomics, proteomics, and metabolomics to elucidate the complex molecular networks underlying plasma-induced stress tolerance. Such comprehensive analyses will provide deeper insights into the coordinated cellular responses activated by APNTP treatment. Furthermore, integrating APNTP with complementary sustainable technologies, such as precision agriculture, biochar amendments, or beneficial microorganism inoculation, may yield synergistic effects that enhance overall system resilience. Establishing international collaborative networks and open-access databases documenting standardized treatment protocols and outcomes would accelerate knowledge translation and facilitate evidence-based implementation strategies across diverse agricultural and animal production systems.

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