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REVIEW

Non-thermal plasmas for disease control and abiotic stress management in plants

Susmita C.[1] · S. P. Jeevan Kumar[2] · Anjani Devi Chintagunta[3] · Eric Lichtfouse[4] · Bhojaraj Naik[5] · Ramya P.[5] · Kalyani Kumari[1] · Sanjay Kumar[1]

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Abstract
Climate change is predicted to cause severe loss in agricultural production by increasing disease epidemics and intensifying abiotic stresses. Therefore, there is a need for sustainable methods to alleviate plant stress, such as non-thermal plasma. Here we review the role of non-thermal plasma for plant treatment, with focus on the control of viruses, bacteria, fungi and other diseases. We present factors influencing the microbicidal activity of non-thermal plasma. Application of non-thermal plasma for combating abiotic stresses such as drought, metal toxicity, nanoparticles and salinity are discussed. Plasma-generated reactive species trigger the activity of stress-responsive genes in plants. The hypothetical mechanisms involved in triggering the activity of different stress-responsive genes controlling diseases as well as abiotic stresses, are also presented and discussed. The mechanism of plant-plasma interaction is similar to priming, hormesis or adaptive response, and resembles vaccination in animals and humans.

Keywords Climate change · Disease · Abiotic stress · Non-thermal plasma · Reactive oxygen and nitrogen species · Oxidative stress · Stress-responsive genes

Introduction

Agricultural productivity is jeopardized by several stress factors coupled with climate change (Challinor et al. 2014; Zhao et al. 2017). In the coming decade, agriculture is anticipated to solve challenges such as population rise over 30% and competition for depleting natural resources of land, water and energy (Challinor et al. 2014). In this context, traditional stress management strategies are limited. Plasma agriculture is an emerging field, where the application of non-thermal plasma on plants has demonstrated promising results. Non-thermal plasma is also referred to as cold plasma, low-temperature plasma or non-equilibrium plasma. In non-thermal plasma, the temperature of heavy particles such as ions, neutrals and radicals is much lower than the temperature of electrons (Ji et al. 2019). Hence, thermodynamic disequilibrium arises between heavy particles and electrons, and this unique property enables cold plasma in treating biological materials (Misra et al. 2019).

Although plasma has been frequently used to treat the surfaces of various biological materials, the effects of plasma treatment are not confined to the surface. Indeed, effects are often observed deeper into the living tissues due to activity of reactive species generated from plasma (Lu et al. 2016; Varilla et al. 2020). Non-thermal plasma can be

✉ Susmita C.
susmitha.cherukuri00@gmail.com; jeevanicar@gmail.com

✉ S. P. Jeevan Kumar
susmitha.cherukuri00@gmail.com; jeevanicar@gmail.com

[1] ICAR-Indian Institute of Seed Science, Mau, Uttar Pradesh 275 103, India

[2] ICAR-Directorate of Floricultural Research, Pune, Maharashtra 411 036, India

[3] Department of Biotechnology, Vignan's Foundation for Science, Technology and Research, Vadlamudi, Guntur, Andhra Pradesh 522213, India

[4] CNRS, IRD, INRAE, CEREGE, Aix Marseille University, Aix-en-Provence, France

[5] Regional Station, ICAR-Indian Institute of Seed Science, Bengaluru 560 065, India

produced at either low pressure or atmospheric pressure, which facilitates plasma use in agriculture, food processing, water decontamination and medicine (Ambrico et al. 2020; Babajani et al. 2019; Pérez-Pizá et al. 2021; Puač et al. 2018, Surowsky et al. 2015, Zhang et al. 2018, von Woedtke et al. 2013).

Application of non-thermal plasma in agriculture stimulates plethora of responses in plants during different phases of growth and development (Adhikari et al. 2020a, b; Holubová et al. 2020). In addition to enhancing seed germination and seedling growth, pre-treatment of planting material with non-thermal plasma showed alleviation of several stress factors (Fig. 1). Recent research focussed on deciphering the role of non-thermal plasma in food processing, and in stimulating seed germination and seedling growth (Pignata et al. 2017; Sonawane and Patil 2020; Cui et al. 2019; Măgureanu et al. 2018; Starič et al. 2020). Nevertheless, the use of non-thermal plasma to manage stress crop plants has been rarely analyzed. Therefore, here we review the use of non-thermal plasma to treat crop plants with focus on mechanisms ruling pathogen control and abiotic stress tolerance.

Mechanism of non-thermal plasma in alleviating plant stress

Ideal conditions for plant growth occur rarely in nature, compared to unfavorable conditions. Hence, plants have evolved certain mechanisms that empower them to actively safeguard from broad range of biotic and abiotic stressors (Zhu 2016). In general, an intense stress is a burden on any living organism, especially plants. Yet, low intensity stress forces plants to activate defense-related pathways, as long as the strength of the stress signal remains weak and affordable (Hilker et al. 2016). Non-thermal plasma action on plants represents a biphasic response and resembles the processes of priming, hormesis, or adaptive response, that in some way remain identical to vaccination responses seen in humans and animals (Pastor et al. 2013; Holubová et al. 2020).

Application of non-thermal plasma in agriculture has been widely reported to stimulate a variety of responses in plants during different phases of growth and development (Adhikari et al. 2020a, b; Holubová et al. 2020). Pretreatment of seeds and seedlings with non-thermal plasma enhances germination and growth and alleviates stress.

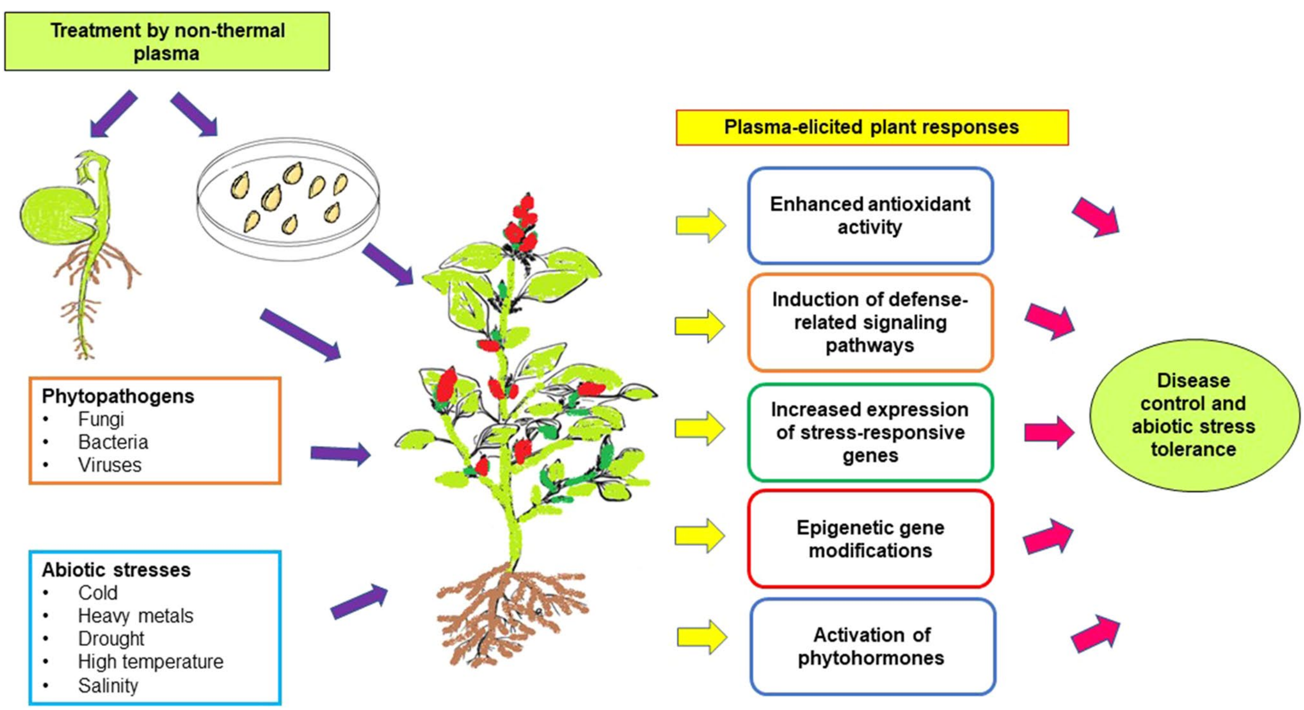

Fig. 1 Non-thermal plasma induces responses in plants, which promote tolerance against disease and abiotic stress. Usually seeds or seedlings are treated with plasma that eventually triggers the activity of antioxidants and phytohormones, activate stress-signaling pathways and related gene expression, and induce epigenetic modifications

Therefore, exposure of biological material to the mild stress of plasma reactive species induces protection against stronger stress (Esposito et al. 2011). However, the intensity of initial plasma stress should be carefully tuned to activate defense responses without seed deterioration (Agathokleous et al. 2019; Agathokleous and Calabrese, 2019). Thus, optimization of physical parameters of the plasma is critical to generate plasma components in appropriate doses for achieving a desired biological response (Szili et al. 2015; Sthijns et al. 2016; Tabares and Junkar 2021).

Methods for plant disease management

Conventional methods

Plants encounter several biotic stresses throughout their life cycle due to the confrontation of other living organisms such as fungi, bacteria, viruses, insects and weeds that severely impede their growth and development resulting (Horst, 2001). An average of 10-16% loss of crop production, equivalent to half a billion tonnes of food, occurs every year due to plant diseases (Strange and Scott 2005; Oerke, 2006). The annual monetary loses due to plant diseases is around $220 billions worldwide (FAO 2019). Hence, the control of plant diseases is essential for sustainable food production (Strange and Scott 2005). Selective breeding for the development of resistant varieties and application of agro-chemicals is common but has limitations. Breeding plants to develop new resistant varieties that possess constitutively active defense is not a viable option. Since, there are known fitness costs associated with the stimulation of defense responses in plants (Heil et al. 2000; Huot et al. 2014). Large-scale application of chemicals to crops causes environmental pollution (Hahn, 2014; Dhananjayan et al. 2020). Moreover, the overuse of resistant varieties and chemical formulations on plants induce the breakdown of disease resistance with risk of emergence of new races of pathogens (Jørgensen et al. 2017). Biocontrol agents are also able to inhibit phytopathogens (Heimpel and Mills 2017). Nonetheless, implementation of biocontrol agents on a commercial scale for plant disease management is constrained in terms of reliability, efficiency, durability and cost (Pal and Gardener 2006). Thus, conventional technologies have often limitations of environmental safety, efficiency and economical aspects.

Non-thermal plasma

Existing research evidence strongly suggest non-thermal plasma technology as an eco-friendly approach for management of various stress factors encountered by plants. Application of non-thermal plasma for inactivation of fungal and bacterial pathogens causing food contamination has been frequently demonstrated (Puligundla and Mok 2016; Misra et al. 2019). Besides, the role of non-thermal plasma in controlling human and animal viruses was also reported (Filipić et al. 2020). However, the potentiality of plasma technology in the deactivation of plant pathogenic fungi, bacteria and viruses has been comparatively less explored. Few studies reported effective inactivation of fungi, bacteria and viruses in different crop species (Table 1). In these studies, different combinations of gases and plasma sources are utilized to eradicate phytopathogens under laboratory conditions, as discussed below.

Non-thermal plasma treatment for the control of fungal pathogens

Seed-borne diseases Seed contamination with pathogenic microorganisms causes diseases in seedlings, leading to a significant reduction in crop yield (Oerke 2006). Indeed, the quality of seeds alone accounts for at least 10-15% increase in the total crop productivity (Gupta and Kumar 2020). Thus, planting disease-free seeds could minimize the losses. Both pre-sowing and post-harvest treatments of seeds are critical for disease management in plants. Pre-sowing treatment of seeds using plasma eradicates fungal pathogens and restricts the inoculum build-up on seed surface and progression of disease after germination (Adhikari et al. 2020a, b; Pignata et al. 2017).

Application of non-thermal plasma for the control of seed-borne diseases has been mostly performed by exposing the seeds either directly to plasma, or through plasma generated gas/plasma-activated water (Selcuk et al. 2008; Nishioka et al. 2014; Brasoveanu et al. 2015; Kordas et al. 2015; Khamsen et al. 2016; Ambrico et al. 2017; Ochi et al. 2017). In most of the studies, direct plasma treatment was frequently performed on the seeds for the control of diseases. Alternatively, plasma can be applied directly on the suspension cultures prepared in vitro for the inactivation of fungal spores and mycelial growth (Avramidis et al. 2010; Na et al. 2013; Hashizume et al. 2014; Panngom et al. 2014).

Avramidis et al. (2010) evaluated the effects of air plasma treatment on the vegetative state (the hyphae) of fungal species and found remarkable inhibition in growth as well as deformation and disruption of fungal hyphae. Similarly, Na et al. (2013) reported a drastic reduction in hyphal growth and spore germination of two fungal species, viz., *Neurospora* sp. and *Fusarium* sp., following the application of a microwave plasma jet. Nonetheless, other studies, using various modes of plasma discharge, reported only partial deactivation of pathogens. For instance, non-thermal plasma generated using diffuse co-planar surface barrier discharge resulted in the reduction few microorganisms and pathogens

Table 1 Published data on the effect of non-thermal plasma treatment in inducing disease stress resistance and microbial inactivation efficiency in various plant species

Treated material	Type of plasma	Target organism	Impact summary	Reference
Fungal diseases				
Philodendron erubescens leaves	Atmospheric cold plasma jet using helium/oxygen	*Colletotrichum gloeosporioides*	Oxidative radicals produced from plasma could disrupt oil vacuoles, polysaccharides, and proteins inactivating the fungus	Zhang et al. (2007)
Cereals and pulses	Low pressure cold plasma using air gases and sulfur hexafluoride	*Aspergillus* sp. and *Pencillium* sp.	Plasma treatment for 15 min using sulfur hexafluoride could significantly reduce microbial colonies to 3-log in both the fungal species	Selcuk et al. (2008)
Fungal spore suspension	Atmospheric pressure dielectric barrier discharge plasma	*Aschocyta pinodella* and *Fusarium culmorum*	Treatment could significantly inhibit the vegetative state of fungi as well as deform and disrupt the fungal hyphae	Avramidis et al. (2010)
Spring wheat, maize and blue lupine	Low pressure capacitively coupled radio frequency plasma	*Fusarium* sp., *Alternaria* sp., *Pencilium* sp., *Cladosporium* sp., *Colletotrichum gloeosporioides*, *Mucor* sp. and *Kabatiella caulivora*	Treatment displayed a fungicidal effect on grain and legume seeds, and the initial fungal infection load was declined by 3-5%	Filatova et al. (2011)
Fungal spore suspension	Microwave plasma jet	*Fusarium graminearum, Fusarium oxysporum* and *Neurospora crassa*	Spore germination and hyphal growth of the fungi were dramatically decreased by using oxygen in the plasma discharge. Variable levels of inhibition on spore germination and growth were noticed among the three fungal species	Na et al. (2013)
Rice seeds	Atmospheric pressure dielectric barrier discharge plasma	*Gibberella fujikuroi*	Inhibition in the growth of fungus and reduction in the number of fungal colonies on the treated seeds by more than 92%	Jo et al. (2014)
Tomato seeds and fungal spore suspension	Atmospheric pressure plasma jet	*Cladosporium fulvum*	Significant reduction in the rotting of infected seeds due to degradation of fungal protein and DNA	Lu et al. (2014)
Brasssicaceous seeds	Both atmospheric pressure and low pressure plasma	*Rhizoctonia solani*	Treatment with atmospheric plasma for 10 min markedly reduced fungal survival rate to 3% but delayed seed germination	Nishioka et al. (2014)
Tomato seeds	Micro dielectric barrier discharge plasma using air/argon	*Fusarium oxysporum f. sp. lycopersici*	Significant reduction in spore germination percent after 10 min of treatment	Panngom et al. (2014)
Barley and corn seeds	Glow discharge plasma	*Aspergillus* sp., *Penicillium* sp. and *Fusarium* sp.	Fungal load on the seeds of both crop species decreased significantly with an increase in treatment duration	Brasoveanu et al. (2015)
Rice seeds	Arc discharge plasma	*Fusarium fujikuroi*	Reactive species generated from plasma played an important role in reducing *fungal load*	Kang et al. (2015)

Table 1 (continued)

Treated material	Type of plasma	Target organism	Impact summary	Reference
Wheat seeds	Low-temperature plasma	*Alternaria* sp., *Fusarium* sp., *Gibberella* sp., *Pencillium* sp., *Rhizopus stolonifera*, *Trichoderma* sp. and non-spore forming fungi	Treatment could reduce the number of fungal colonies to the order of 1-log within 10 s of exposure	Kordas et al. (2015)
Hazelnut	Atmospheric pressure fluid bed plasma	*Aspergillus flavus* and *Aspergillus parasiticus*	A significant reduction in the inoculum load of both the fungi *A. flavus* and *A. parasiticus* to the extent of 4.5-log and 4.19-log, respectively, was reported using air as plasma gas	Dasan et al. (2016)
Rice seed husk	Atmospheric pressure hybrid micro corona discharge plasma	Infected microbes	Complete inactivation of pathogenic fungi along with other microorganisms; Positive impact on seed germination and seedling growth was noticed	Khamsen et al. (2016)
Wheat seeds	DCSBD plasma	*Fusarium* sp., *Tricothecium roseum* and *Aspergillus* sp.	The growth inhibition effect of plasma on the surface microflora of seeds increased with the enhancement in the treatment time and power intensity	Zahoranová et al. (2016)
Sweet basil seeds	Surface dielectric barrier discharge plasma	Infected fungi	Treatment for 20 s significantly reduced the microbial load without affecting seed viability	Ambrico et al. (2017)
Rice seeds	Atmospheric pressure plasma jet	*Fusarium fujikuroi*	Disease severity index of fungus reduced to 18.1% after plasma treatment	Ochi et al. (2017)
Cucumber and Pepper seeds	DCSBD plasma using ambient air	*Cladosporium cucumerinum* and *Didymella bryoniae*	Treatment for 20 s in cucumber could completely eradicate spores of *Cladosporium* sp., whereas 60-80% reduction in spores of *Didymella* sp. was noticed. In pepper, 50-80% reduction in the spores of *Didymella* sp. was noticed after 4 s of treatment	Štěpánová et al. (2018)
Barley and wheat seeds	High voltage dielectric barrier discharge plasma	Native microbes (both fungi and bacteria), artificially challenged microbes (bacteria)	Significant reduction in the load of inoculated challenge populations was observed in wheat and barley grains, as compared to natural microbiota	Los et al. (2018)
Soybean seeds	Atmospheric pressure dielectric barrier discharge plasma using nitrogen/oxygen	*Diaporthe/ Phomopsis* complex	Reversal of oxidative damage caused by fungal complex in the treated seeds was noticed	Pérez Pizá et al. (2018)
Pine seeds	DCSBD plasma	*Fusarium circinatum*	Complete deactivation of fungus was observed after 60 s of treatment	Šerá et al. (2019)

Table 1 (continued)

Treated material	Type of plasma	Target organism	Impact summary	Reference
Fungal spore suspension	Atmospheric pressure corona PAW	*Colletotrichum gloeosporioides*	Inactivation rate of fungus was higher using air-PAW than oxygen-PAW, and microbicidal efficiency enhanced with increase in treatment duration	Wu et al. (2019)
Maize seeds	DCSBD plasma	*Aspergillus flavus, Aspergillus alternata* and *Fusarium culmorum*	Reduction in colonies of *F. culmorum* by 3.79-log after 60 s of treatment was noticed; while *A. flavus* and *A. alternata* were reduced by 4.21-log and 3.22-log, respectively, after treating for 300 s	Zahoranová et al. (2018)
Winter wheat, narrow-leaved lupine and maize	Low pressure radio frequency plasma	Boil smut and root rot fungi	Treatment could induce suppression of fungal colonies and increase the activity of non-enzymatic antioxidants enhancing disease resistance	Filatova et al. (2020)
Fungal spores	Dielectric barrier discharge using nitrogen or oxygen	*Diaporthe longicolla*	Plasma-induced lipid peroxidation and antioxidant activity severely affected the growth of fungal colonies	Pérez-Pizá et al. (2021)
Bacterial diseases				
Suspension culture	Gliding arc discharge plasma	*Erwinia caratovora*	Reported glid-arc discharge to be more effective in killing bacterial colonies without lag time	Moreau et al. (2007)
Tomato seeds	Inductive Helium plasma	*Ralstonia solanacearum*	Significant increase in resistance against bacteria and improvement in antioxidants and hydrogen peroxide concentration	Jiang et al. (2014)
Suspension culture	Low-temperature atmospheric pressure glidarc discharge	*Clavibacter michiganensis* subsp. *michiganensis* and *Erwinia amylovora*	Plasma treatment for 12 min could effectively slow down the growth and reproduction rate of both the bacterial species	Mráz et al. (2014)
Wheat seeds	Atmospheric pressure dielectric barrier discharge plasma	*Geobacillus stearothemophilus*	Reported direct effects of plasma generated species and identified chemical sputtering to be the predominant inactivation mechanism involved in bacterial decontamination	Butscher et al. (2016)
Cabbage seeds	Low pressure plasma using Argon	*Xanthomonas campestris*	Noticed significant reduction in inoculum load by 3.9-log after 5 min of treatment, and complete inactivation of bacteria after 40 min of treatment	Nishioka et al. (2016)
Hydrophonic solution	Discharge plasma reactor	*Ralstonia solanacearum*	Reported significant reduction in the bacterial spore density from 10^7 to 10^2 CFU/ml after plasma treatment using atmospheric gases	Okumura et al. (2016)

Table 1 (continued)

Treated material	Type of plasma	Target organism	Impact summary	Reference
Rice seeds	Atmospheric pressure plasma jet	*Burkholderia plantarii*	Disease severity index reduced to 38.6% in the treated seeds	Ochi et al. (2017)
Suspension culture	Roller conveyer atmospheric pressure plasma	*Xanthomonas campestris* pv. *campestris*	Viable bacterial cells decreased exponentially from 5.0×10^8 to 9.8×10^5 CFU/ml with a reduction in treatment time from 0.90 min to below 0.34 min	Toyokawa et al. (2017)
Suspension culture	DC-APGD	*Clavibacter* sp., *Dickeya solani*, *Xanthomonas* sp. and *Pectobacterium* sp.	Treatment with plasma induced complete destruction of three bacterial species; while partial reduction in colonies of *Pectobacterium sp.* was noticed	Motyka et al. (2018)
Viral diseases				
Romain lettuce leaves	Cold atmospheric plasma generated from dielectric barrier discharge	Tulane virus and bacterial species	Significant degree of anti-viral activity and reduction in bacterial load was noticed after plasma treatment	Min et al. (2016)
Bacteriophage suspensions	Cold atmospheric plasma and plasma-activated water	T4, Φ174 and MS2 viral strains	Treatment could induce aggregation of bacteriophages and damage to nucleic acid and proteins of virus	Guo et al. (2018)
Tobacco leaves	Cold atmospheric plasma generated from air	Tobacco mosaic virus	Treatment could potentially inactivate viral particles and leaves inoculated with virus that were pre-treated with plasma failed to develop necrotic lesions	Hanbal et al. (2018)
Irrigation water	Cold atmospheric plasma generated from argon and oxygen	Potato virus Y	Plasma treatment could induce degradation of viral genetic material	Filipić et al. (2019)

DCSBD diffuse co-planar surface barrier discharge, *DC-APGD* direct current-atmospheric pressure glow discharge, *CFU/ml* colony-forming units per millilitre, *PAW* plasma-activated water, *s* seconds, *min* minutes on seed surface (Štěpánová et al. 2018). Results showed partial deactivation of *Didymella lycopersici* in both cucumber and pepper. But, the viral load present on the seed surface remained unaffected by plasma treatment.

Foliar and root diseases Foliage and root diseases are serious plant diseases that cause significant reduction in the crop's yield and quality. There have been various epidemics caused by foliar diseases in the history of agriculture, for example, the late blight of potato, brown spot of rice, coffee rust and wheat stem rust. In comparison with seed-borne diseases, they are relatively more difficult to treat with plasma, since the plant tissues are sensitive and easily liable to damage (Zhang et al. 2014; Seol et al. 2017).

Panngom et al. (2014) tested the antimicrobial efficacy of dielectric barrier discharge plasma treatment using air/argon, against wilt pathogen *Fusarium oxysporum* f. sp. *lycopersici* in tomato. After plasma treatment, a significant reduction in fungal spore density was observed. Findings were explained by the generation of reactive nitrogen species in inducing necrotic spore death by the production of toxic peroxynitrite and nitrate. Moreover, the transcriptional profiling of pathogenesis-related genes, viz., pathogenesis-related gene-1a (PR1a), pathogenesis-related gene-1b (PR1b) and pathogenesis-related gene-3a (PR 3a) from tomato roots, disclosed that reactive oxygen species are responsible for the up-regulation of defense-related genes in plants and the induction of apoptosis-like death in fungal spores. Yet, the study also reported that the same dosage of plasma could potentially induce contradictory effects, by inactivation of defense mechanisms in pathogen and simultaneously activate the resistance mechanisms in host.

Cold plasma treatment on fungus-infected leaves of *Philodendron erubescens* reversed infected spots to normal state in treated leaves. Further, enhanced disruption of oil vacuoles, polysaccharides and protein molecules of the fungus *Colletotrichum gloeosporioides* resulted from the oxidative damage caused by reactive species (Zhang et al. 2014). Jiang et al. (2014) identified noticeable improvement in seedling germination and resistance against bacterial wilt in tomato through plasma treatment. Leaves of treated plants displayed higher concentrations of hydrogen peroxide (H_2O_2) and improvement in the activity of defense enzymes such as peroxidase, polyphenol oxidase and phenylalanine ammonia lyase, as compared to untreated plants.

Non-thermal plasma treatment for the control of bacterial pathogens

Although plant pathogenic bacteria cause less diseases in crop plants than fungal and viral pathogens, bacteria are equally problematic and cause significant economic losses worldwide (Sundin et al. 2016). Several studies reported that non-thermal plasma treatment of phytobacterial suspensions inhibits the growth and number of bacteria (Moreau et al. 2007; Mráz et al. 2014; Toyokawa et al. 2017; Motyka et al. 2018). Mráz et al. (2014) reported that exposure to plasma could decelerate the growth and reproduction of both gram-positive and gram-negative bacteria. The pathogenicity and the colony-forming capability of *Ralstonia* sp. was decreased by plasma discharged through a hydroponic solution (Okumura et al. 2016). Toyokawa et al. (2017) reported the reduction in the viability of *Xanthomonas* sp. exposed to roller plasma conveyer, as a consequence of the degradation of lipopolysaccharides and the oxidation of DNA.

Motyka et al. (2018) investigated the antibacterial properties of plasma generated from direct current-atmospheric pressure glow discharge against five bacterial species, viz., *Clavibacter michiganensis* subsp. *sepedonicus*, *Dickeya solani*, *Xanthomonas campestris* pv. *campestris*, *Pectobacterium atrosepticum* and *Pectobacterium carotovorum* subsp. *carotovorum*. While complete eradication of *Clavibacter* sp., *Dickeya* sp. and *Xanthomonas* sp. was achieved after plasma treatment, a reduction up to 3.43 fold in the inoculum density of *Pectobacterium* sp. was noticed. Further, the study reported that ultra-violet radiation A-C exerted a bactericidal activity following production of reactive species. Treatment with plasma-based nanoparticles such as fructose-stabilized silver nanoparticles, produced by direct current-atmospheric pressure glow discharge, also exerted antibacterial effects on the growth and reproduction of strains belonging to *Erwinia* sp., *Clavibacter* sp., *Ralstonia* sp., *Xanthomonas* sp. and *Dickeya* sp. (Dzimitrowicz et al. 2018).

Non-thermal plasma treatment for control of viral diseases

Compared to bacterial and fungal pathogens, the use of non-thermal plasma in controlling viral diseases of plants has been rarely attempted, whereas applications on human and animal viruses are reported (Puligundla and Mok, 2016). Min et al. (2016) found that dielectric barrier discharge plasma treatment on leaves of romaine lettuce could reduce up to 90%, the infection caused by Tulane virus. Similarly, Hanbal et al. (2018) stated that inoculation with plasma irradiated tobacco mosaic virus solution on the leaves of tobacco could suppress the disease progression, whereas plants inoculated with the virus not exposed to plasma irradiation developed necrotic lesions on the leaves.

Plasma-activated water for management of phytopathogens

Distilled water exposed to cold plasma, often termed as plasma-treated water or plasma-activated water, exhibits an anti-microbial activity (Perez et al. 2019; Wu et al. 2019). Wu et al. (2019) reported that plasma-activated water produced using air and oxygen as gaseous sources could potentially deactivate the fungal spores of *Colletotrichum gloeosporioides*. However, among the substrate gases used, air was found to be more effective than dioxygen in generating toxic reactive species. Among the reactive species, nitrate and ozone produced from plasma played a major role in spore destruction. Non-thermal plasma has been proposed to act as a priming agent (Babajani et al. 2019; Adhikari et al. 2020a, b). Adhikari et al. (2019) stated that priming with plasma-activated water could enhance seedling growth, endogenous reactive oxygen and nitrogen species activity in tomato seedlings. In addition, induction of defense hormones, e.g., salicylic acid and jasmonic acid, and up-regulation in the expression of key pathogenesis-related genes, β-1,3 glucanase, chitinase-3-acid, mitogen-activated protein kinase and redox homeostasis genes were observed.

Plasma treatment also minimizes bacterial contamination in water or waste that often acts as disease inoculum source. Indeed, plasma treatment of water systems induced sub-lethal state of bacteria to viable but non-culturable state, but complete decontamination was not achieved (Xu et al. 2018). Bertaccini et al. (2017) stated that the treatment with plasma-activated water could trigger defense responses in grapevine against diseases caused by phytoplasmas, which are phloem-limited pleomorphic bacteria devoid of cell wall. By contrast, Perez et al. (2019) revealed application of plasma-activated water had no direct antimicrobial effects against *Xanthomonas vesicatoria*. However, the treatment could reduce bacterial infection rate in treated plants by intensifying the expression of disease resistance genes in the host. Filipić et al. (2019) noticed that application of plasma on irrigation water favors the complete inactivation of Potato virus Y, a water transmissible plant virus. Hence, non-thermal plasma treatment could be used as a potential alternative for controlling the viruses that can spread through water systems. Similarly, Guo et al. (2018) reported reduction in the infection rate of bacteriophages in water samples exposed to non-thermal plasma.

Factors controlling the microbicidal activity of non-thermal plasma

Treatment duration

Finding the optimal time of seed disinfection by plasma treatment is challenging. Several studies reported that plasma has no adverse effects on seed germination and subsequent growth during devitalization of phytopathogens (Selcuk et al. 2008; Jo et al. 2014; Kordas et al. 2015; Khamsen et al. 2016; Štěpánová et al. 2018). Long treatment time improves sterilization (Lu et al. 2014; Zahoranová et al. 2016, 2018; Homa et al. 2021). Bourke et al. (2018) found that longer treatment coupled with higher voltage and frequency promotes microbial decontamination. Nevertheless, Homa et al. (2021) found that longer treatment time could increase the temperature of treated surfaces and, in turn, decrease germination of sweet basil.

Nature of the pathogen

The potential resistance of the pathogen to non-thermal plasma treatment is another important limiting factor. In a study conducted by Zahoranová et al. (2018), seeds of maize were artificially inoculated with harmful species of fungi and bacteria. Subsequent to this, seeds were treated with diffuse co-planar surface barrier discharge plasma. While complete decontamination of bacterial spores was achieved within a short exposure of 60 s, fungal spores were de-vitalized after 180 s. This suggests that there are distinct survival rates of spores among microbial species exposed to non-thermal plasma (Butscher et al. 2016; Zahoranová et al. 2018).

Similarly, Kim et al. (2017) observed varying levels of reduction among microbial species using cold plasma jet. For instance, bacterial species were inactivated faster than molds and yeasts. Further, Los et al. (2018) reported a strong influence of the type of microorganism, e.g., native versus artificially inoculated microbes, and its physiological state on the inactivation efficacy of plasma treatment. Bourke et al. (2018) found higher inactivation rates of artificial surface inoculations of a single pathogen, by comparison with native microflora containing multiple species. Differences observed in the efficiency of microbial inactivation by plasma treatment could be assigned to variations in cytology, morphology, structure of cellular envelopes, reproductive cycle and growth phase (Bourke et al. 2018). The efficiency of plasma treatment was also reported to vary depending on the pathogen propagule (Assaraf et al. 2002; Pérez-Pizá et al. 2021). The conidial stage is more sensitive to plasma treatment compared to chlamydospores in case of *Alternaria* species (Ambrico et al. 2017).

Structure of the treated surface

The microbicidal activity of plasma treatment can also vary based on the type of seed used, its surface characteristics, the genus and species of plants, and the plant-pathogen micro-environment (Selcuk et al. 2008; Lu et al. 2014; Butscher et al. 2016; Niedźwiedź et al. 2019). Few studies suggested partial deactivation of microbes through plasma treatment, due to incomplete exposure of seeds owing to their surface properties, e.g., crevices and micropyle (Ambrico et al. 2017; Homa et al. 2021). Further, Homa et al. (2021) found that dielectric barrier discharge plasma on seeds or direct cold plasma jet treatment on seedlings is highly effective in controlling the virulence and mycelial growth of *Fusarium oxysporum* in basil, as compared to plasma treatment directly on the in vitro cultures of fungi.

Type of plasma discharge

Plasma-generated species vary based on the conditions of plasma discharge, and this further controls the microbial inactivation processes. Nojima et al. (2007) developed a plasma device generating atomic hydrogen (^1H) and demonstrated that ^1H surrounded by water molecules, *i.e*., $H(H_2O)_m$, played a key role in the deactivation of air-borne microbes, probably due to its long life. $H(H_2O)_m$ released from the device reacted with oxygen (O_2) and superoxide anion (O_2^-) surrounded by $(H_2O_2)_n$, generating highly reactive secondary species such as hydroperoxyl radical (HO_2) and dioxidanide (HO_2^-), which further exerted cytotoxic effects on microbes.

Many researchers reported that dielectric barrier discharge type plasma is more effective than other discharge types for fungal spore eradication (Avramidis et al. 2010; Iseki et al. 2011; Hashizume et al. 2014; Panngom et al. 2014). Low pressure plasma treatment is highly effective for complete disinfection of bacterial spores from vegetable seeds (Nishioka et al. 2016). Kang et al. (2020) reported that rice seeds treated with underwater arc discharge plasma and surface dielectric barrier discharge plasma in air (in presence of H_2O_2) at low pressure had higher disinfection rates against *Fusarium fujikuroi*. Therefore, standardization of plasma parameters, *i.e.,* source of discharge, treatment time, dose, pressure, frequency and electrode configuration, is equally crucial for fine-tuning plasma application.

Possible role of plasma components in stimulating the microbial inactivation

Non-thermal plasma has been widely reported to generate ultra-violet rays, charged particles, metastables, electromagnetic radiation and a variety of reactive species. These cocktail of plasma components exert severe microbicidal activity against phytopathogens. They tend to inactivate microbes either directly by the action of ultra-violet and vacuum ultra-violet irradiation, or indirectly through the activity of reactive species (Tensmeyer et al. 1981; Nelson and Berger 1989; Lu et al. 2014).

Ultra-violet radiation

The microbicidal efficiency of ultra-violet radiation on any biological material largely depends on the dose delivered to the surface (Martin et al. 2008). The dose, in micro- or milliJoules per square centimeter, of ultra-violet radiation needed to disinfect a surface varies depends on the selected target and desired disinfection levels (Brickener et al. 2003). Different microorganisms require various doses of ultra-violet energy for inactivation. For instance, vegetative forms of bacteria tend to be highly susceptible to ultra-violet radiation as compared to spore-forming microbes (Kowalski 2009). Non-thermal plasma produces ultra-violet radiation with different wavelengths. Few studies suggest that not all wavelengths of ultra-violet radiation are effective to inactivate microorganisms (Laroussi and Leipold 2004; Deng et al. 2006; Lee et al. 2005; Dobrynin et al. 2009). Generally, ultraviolet radiation in the range of 200-300 nm with doses of several milliJoules per square centimeter is known to be lethal and cause damage to microbial cells (Laurossi 2005; Fridman 2008).

The efficiency of ultra-violet radiation generated from the plasma also strongly depends on the operating pressure. Vacuum plasma discharges generate ultra-violet radiation with wavelengths effective for sterilization. Hence, ultra-violet radiation is considered as a chief contributor in vacuum plasma sterilization (Moisan et al. 2001, 2002). Similarly, ultra-violet C produced from low pressure vacuum plasma at 200-280 nm is effective for sterilization of biological tissues and inactivation of microbes (Boudam et al. 2006; Motyka et al. 2018). On the contrary, photons generated from atmospheric or high pressure plasma systems do not play a significant role for sterilization as they emit insufficient doses of ultra-violet radiation (De Geyter and Morent 2012; Misra et al. 2019). Many studies hypothesized that atmospheric pressure plasma generated ultra-violet rays alone should adequately inactivate bacterial spores (Trompeter et al. 2002; Park et al. 2003; Birmingham, 2004; Heise et al. 2004; Lee et al. 2005; Boudam et al. 2006; Deng et al. 2006). However, other researchers believed that exposure to plasma generated ultra-violet rays alone had negligible microbicidal effects (Patil et al. 2014; Surowsky et al. 2014; Reineke et al. 2015). Hence, further investigation is necessary to clear up the contrasting hypotheses.

Reactive species

Many plasma devices use inert gases such as neon, argon or dinitrogen as feed gas. Although these gases are rather inert, electric discharge into these gases induce their atoms to reach the metasable, an excited state with relatively long shelf life. This state is essential in chemical and ionization processes, and in discharge dynamics (Lu et al. 2016). Based on the substrate gas used, several reactive species are created either within the plasma, or based on plasma interaction with the surrounding atmosphere (Na et al. 2013; Zhang et al.

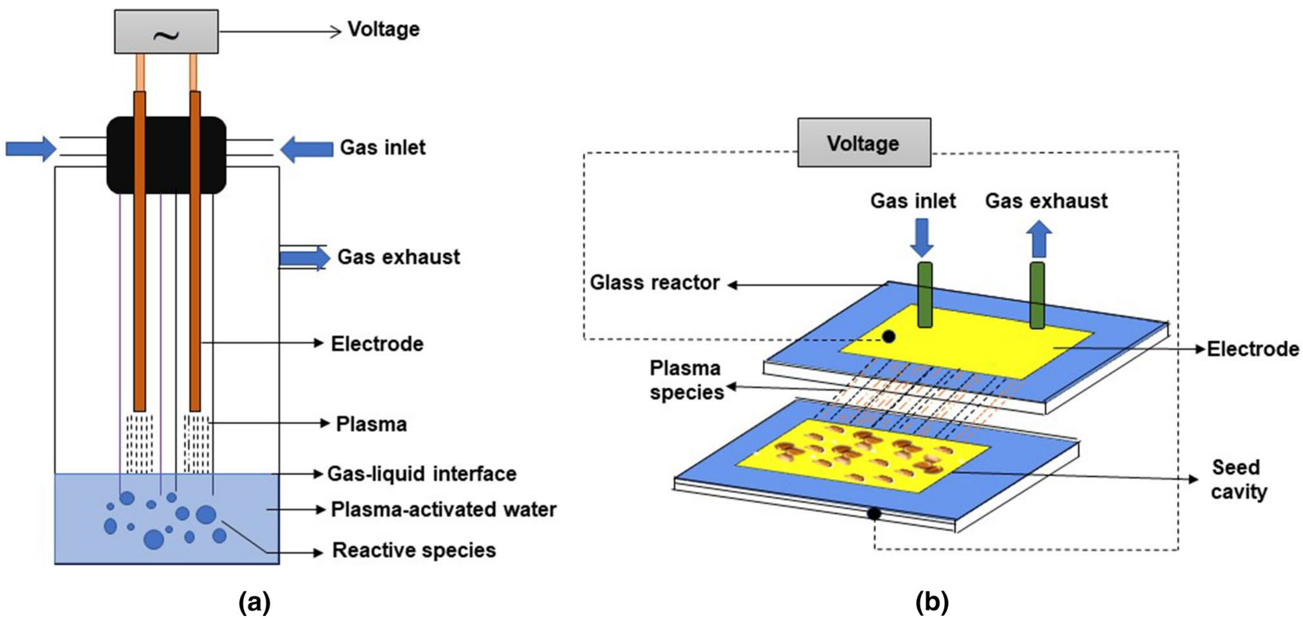

Fig. 2 Schematic illustration of plasma-based treatment of **a** water and **b** seed. **a** Synthesis of plasma-activated water by exposing water to plasma that is used for aqueous treatment (soaking or watering) of seeds or seedlings, **b** treatment of seeds either directly with the plasma or indirectly by placing the seeds at a sufficient distance from the plasma. (Adopted and re-drawn from Sivachandiran and Khacef 2017)

2014; Panngom et al. 2014; Perez et al. 2019). The resulting reactive species include atomic, radical, ionic and molecular species such as atomic oxygen (O), ozone (O_3), singlet oxygen ($^1O_2$), hydroxyl radical ($^{\bullet}OH$), superoxide radical ($O_2^{\bullet-}$), nitric oxide ($^{\bullet}NO$/NO), peroxynitrites ($ONOO^-$ and $OONOO^-$), H_2O_2, nitrites and nitrates (NO_2^- and NO_3^-).

The primary reactive oxygen and nitrogen species such as $^{\bullet}OH$, NO, H_2O_2, O and O_3 are mainly created in the gas phase plasma. If this plasma is discharged through liquid surfaces, the primary reactive species undergo transformations in the liquid by degrading or interacting with each other, or with the molecules in the liquid media to generate secondary reactive species (Gorbanev et al. 2018). Sometimes, the secondary reactive species may also be generated in the gas-liquid interface layer of aqueous solutions (Fig. 2). Reactive oxygen and nitrogen species induce responses in biological substrates and, in turn, allow to control phytopathogens (Heil et al. 2000; Panngom et al. 2014; Puligundla et al. 2017).

The composition of reactive species generated also varies depending on the mode of plasma treatment. For example, non-thermal plasma can be delivered onto the biological targets either by indirect/afterglow or by direct/glow mode. During indirect plasma treatment, the initial liquid medium is pre-treated with non-thermal plasma and then applied onto a biological target (Bermúdez-Aguirre et al. 2013; Puligundla et al. 2017). The biological target may also be exposed outside the area of discharge, yet close enough to interact with plasma generated species (Starič et al. 2020). In this case, the effects of plasma could be chiefly attributed to long-lived molecular and ionic chemical species, e.g., O_3, H_2O_2, NO_2^- and NO_3^-, and secondary reactive species (Panngom et al. 2014; Guo et al. 2018). Therefore, the targets are not exposed directly to radiation and remain in contact with long-lived species that are less aggressive in nature and possess marginal kinetic energy.

The second mode of application involves direct plasma treatment on the biological target, e.g., seeds are placed in a liquid medium or directly exposed within the area of discharge (Bermúdez-Aguirre et al. 2013; Puligundla et al. 2017). Here, the targets are subjected to reactive species comprising both long- and short-lived species, e.g., O, $^{\bullet}NO$, $^{\bullet}OH$ and $O_2^{\bullet-}$, non-radical chemical compounds such as singlet oxygen ($^1O_2$), positive and negative charged particles, neutrals, and ultra-violet/vacuum ultra-violet radiation (Starič et al. 2020). Xiong et al. (2017) showed the major role of short-lived reactive species, e.g., $^{\bullet}OH$, in exerting bactericidal effects, versus long-lived species, e.g., H_2O_2. Among various by-products generated, peroxynitrous acid (ONOOH) was considered to display high antimicrobial activity (Xiong et al. 2017; Perez et al. 2019).

Plasma-generated reactive species can perform many actions on microbial surfaces, such as lipid peroxidation resulting in the modification of the cell membrane composition, reduction in membrane fluidity, alteration in cell permeability and destabilization of membrane proteins.

These reactions ultimately induce the loss of viability and pathogenicity in microbes (Laroussi and Leipold 2004; Joshi et al. 2011). Furthermore, stable reactive species that possess extended cytotoxic activity can disseminate from the membrane toward DNA and react with nucleotides, driving cellular damage and make DNA repair highly detrimental (Yost and Joshi 2015; Rio et al. 2005). In contrast with the activities exerted on phytopathogens, reactive oxygen and nitrogen species could act as signaling molecules in plants for triggering defense-related responses (Adhikari et al. 2020a).

Charged species

Although the overall antimicrobial activity of cold plasma is known, the contribution of each plasma component to the antimicrobial activity is unclear. Besides reactive species, charged species also contribute to microbial decontamination (Dobrynin et al. 2009; Klämpfl et al. 2012). Few researchers proposed that charged particles induce the rupture of the outer membrane of bacterial cells (Mendis et al. 2000; Stoffels et al. 2008). In addition, mechanical erosion of the microbial cellular envelopes could occur due to the impact of the high energy plasma particles such as electrons and excited atoms (Butscher et al. 2016). Sometimes aggregation of charges on particular regions of the microbial cell surface may occur, thus increasing the permeability of cells, termed electroporation (Laroussi et al. 2003).

Overall, the mechanisms ruling the inactivation of phytopathogens involve harmful effects of plasma-generated reactive species, charged particles and ultra-violet photons that target cell membranes and cellular proteins, leading in particular to subsequent denaturation of microbial DNA (Lu et al. 2014; Hertwig et al. 2018). Physico-chemical changes on the cell surface also cause damage to microbes, leading to their deactivation (Sugimoto et al. 2008; Deora et al. 2011; Lu et al. 2014; Pérez Pizá et al. 2018). Among various components of plasma, reactive species are widely reported to be actively involved in causing oxidative damage to intracellular macromolecules of pathogens. Besides, in plants, reactive oxygen and nitrogen species are widely reported as key signaling molecules that have the capability to regulate disease stress through activation of plant defense systems (Simontacchi et al. 2015; Dietz et al. 2016).

Selective effects of plasma-generated reactive species on plant and microbial cells

In order to have a definite understanding of the plasma-mediated disease control, comprehensive knowledge on the interaction of plasma-generated reactive species with plant and microbial cells stands as a key pre-requisite. Primary reactive oxygen and nitrogen species can either impact microbial cells directly or interact with the medium located between plant and microbial cells to produce secondary reactive species (Adhikari et al. 2020a, b). Here, it is expected that the produced oxidative stress alters more the microbial pathogens than the plant cells, because plant cells tolerate oxidative stress better than microbial cells (Dobrynin et al. 2009; Gay-Mimbrera et al. 2016). Indeed, prokaryotic plant pathogens, notably bacteria, possess naked DNA and thus remain more sensitive to plasma treatment than the eukaryotic plant cells (Holubová et al. 2020). Similarly, long-term exposure to plasma-generated reactive species is likely to rise reactive oxygen and nitrogen species to levels that defeat the antioxidant capability of microbial cells, while plant cells maintain homeostasis (Adhikari et al. 2020a, b). Reactive oxygen and nitrogen species display a peculiar role during plant-pathogen interactions. They tend to provoke different signaling pathways in the pathogen and host (Panngom et al. 2014). Reactive oxygen species such as $O_2^{\bullet -}$, $OH^{\bullet}$ and H_2O_2 can oxidize key macromolecules of pathogens and devitalize them (Kumar et al. 2015). Reactive species also activate defense-related gene cascade systems including mitogen-activated protein kinase, respiratory burst oxidase homolog and trigger the expression of pathogenesis-related genes in the host plants (Panngom et al. 2014; Adhikari et al. 2019, 2020a). Moreover, activation of jasmonic acid and salicylic acid-mediated defense pathways boosts the systemic acquired resistance and hypersensitive responses in plants (Vanacker et al. 1998; Adhikari et al. 2020a).

Mechanism of non-thermal plasma in promoting inactivation of phytopathogens

Plasma-generated reactive species and other plasma components achieve microbial decontamination by penetration followed by inactivation. During penetration, mechanical erosion and oxidative damage breaks the chemical bonds and proteins on the microbial cell envelopes. Such surface abrasions on microbial cells can occur either by the direct effect of ultra-violet photons or by etching of highly energetic ions and reactive species (Leipold et al. 2010; Butscher et al. 2016).

Microbial cell surface modifications

The flux of plasma-generated reactive oxygen species into microbial cells enhances oxidative stress, resulting in the oxidation of regulatory macromolecules and ultimately cell death (Lackmann and Bandow, 2014; Tiwari et al. 2018). Plasma-generated reactive oxygen species display different modes of action during the devitalization of gram-negative and gram-positive bacteria (Han et al. 2016). For gram-positive strains, higher levels of intracellular reactive oxygen species promote the inactivation of bacterial cells. For gram-negative strains, damage to the cellular membrane is the main cause of lethality (Han et al. 2016). Likewise, charged particles are major compounds involved in the breakage of outer cell membranes, particularly in gram-negative bacteria, which have thin outer membrane and murein layer (Mendis et al. 2000). Overall, microbial death is controlled by substantial build-up of oxidative stress and damage to various cellular structures and macromolecules during the penetration process (Leipold et al. 2010; Kumar et al. 2015). Nonetheless, if the pathogen is strong enough to bear the damage, these processes would at least facilitate the penetration of reactive species into the nucleus of cells and, in turn, alter the microbial DNA and proteins in an irreversible manner (Kumar et al. 2021a, b).

Plasma-elicited deleterious effects on the microbial genome

Many studies revealed reactive species such as H_2O_2, $O_2^{\bullet-}$, $^1O_2$ and NO are main agents involved in microbial inactivation (Takamatsu et al. 2015; Yost and Joshi, 2015; Misra et al. 2019). Yet the contribution of other plasma components should not be discounted (Dobrynin et al. 2009). In general, reactive species at substantial levels stimulate lipid peroxidation. Peroxidation of lipids on the microbial cell surface alters membrane permeability and diminish cell viability (Joshi et al. 2011; Hosseinzadeh-Colagar et al. 2013; Panngom et al. 2014; Pawłat et al. 2018).

Lipid peroxidation also induces the production of intermediate reactive compounds such as peroxyl, hydroxyl radicals and reactive aldehydes including malonaldehyde that serve as secondary toxic messengers (Dobrynin et al. 2009; Joshi et al. 2011; Pérez-Pizá et al. 2021). Aldehydes diffuse easily through the membrane then react with cellular DNA and induce severe cytotoxic effects (Yost and Joshi, 2015; Pérez-Pizá et al. 2021). Indeed, aldehydes induce nucleotide modifications, trigger cross-links between nucleotides and interrupt the cell growth as well as repair mechanisms (Rio et al. 2005). Aldehydes also induce the development of crosslinks in the protein polypeptide chains that ultimately alter the enzymatic activity and membrane bound proteins of microbes (Joshi et al. 2011; Šimončicová et al. 2018). Thus, plasma-induced modifications on the microbial cell surface and deleterious effects on the genetic material allow microbial decontamination.

Speculative signaling pathways inducing defense responses in plant systems

Whether cold plasma affects only the surface of the seed, or promote internal changes in the seed still remains inconclusive. Few studies reported poor permeability of cold plasma into seeds (Niedźwiedź et al. 2019). Yet other studies reported that plasma-induced reactive species and ultra-violet radiation promote plant growth and development under disease stress through inactivation of phytopathogens and activation of defense-related responses in plant cells (Iranbakhsh et al. 2017, 2018a, b; Perez et al. 2019; Adhikari et al. 2020a). Thus, in addition to exhibiting detrimental effects on the phytopathogens, the plasma treatment has the capacity to induce immune responses in plants termed as plasma-induced 'plant vaccination'. This could be achieved perhaps through the preferential activity of reactive species that instigate oxidative burst and constantly activate defense signaling pathways, thus promoting the expression of defense-related genes in plants.

Reactive oxygen and nitrogen species generated from plasma treatment can enter into the plant system either by wounding, mechanical stress induced during direct treatment or through stomatal openings, and then modify various cellular processes (Heil et al. 2000; Filipić et al. 2019). After gaining entry into the plant, reactive species are perceived by plant cells, resulting in the change of concentrations of intracellular reactive species. Here, plasma-generated reactive species are expected to perform similar functions as the reactive species produced from other sources. Therefore, H_2O_2 and oxides of nitrogen (NO_x) generated from plasma should follow similar mechanisms of action as exogenously applied H_2O_2 and NO_x and thus should have a similar impact on plant cells (Antoniou et al. 2016; Thomas and Puthur, 2017).

H_2O_2-mediated signaling and regulation of transcription factors

In general, unstable reactive oxygen species including $O_2^{\bullet-}$ and $^1O_2$ might react with various components of plant cells. Stable reactive oxygen and nitrogen species such as H_2O_2 and NO move into the plant cell wall by diffusion into the apoplast through aquaporins (Jang et al. 2012). They interact with the cell membrane receptors, activating different defense-related genes, proteins and hormones. H_2O_2 is a signaling molecule that mainly targets calcium homeostasis and alters ion channels, transcription factors, kinases and phosphatases by oxidization of the methionine residues of proteins (Ghesquière et al. 2011; Petrov and Van Breusegem, 2012). Moreover, H_2O_2 activates the mitogen-activated protein kinase cascade during plant-pathogen interactions, thus promoting defense gene activation (Zhang et al. 2007; Xing et al. 2008).

H_2O_2 acts by altering the mitochondrial membrane potential and changing the phosphorylated mitogen-activated protein kinase levels in a dose-dependent manner (Zhang and Klessig, 2001; Kaushik et al. 2015). Consequently, mitogen-activated protein kinase phosphorylates key transcription factors such as WRKY and arabidopsis NAC transcription factor (ANAC042) (Petrov and Van Breusegem, 2012). The WRKY name is derived from the highly conserved 60 amino acid long WRKY domains of the transcription factors that possess a novel zinc-finger-like motif at the C-terminus and conserved heptapeptide motif WRKYGQK at the N-terminus (Bakshi and Oelmüller, 2014). The NAC name was coined based on the names of three transcription factors, viz*.,* NAM (no apical meristem of Petunia), ATAF1-2 (Arabidopsis thaliana activating factor) and CUC-2 (cup-shaped cotyledon of Arabidopsis) (Jensen et al. 2010). In the following sections, both the transcription factors are annotated as WRKY and NAC, respectively.

Several other transcription factors, including zinc finger of *Arabidopsis thaliana* (ZAT), dehydration-responsive element binding (DREB) factor, basic leucine zipper (bZIP) and myeloblastosis family (MYB), were also proclaimed to be activated by H_2O_2 signaling, which in turn regulate the expression of defense-related genes (Petrov and Van Breusegem, 2012). Furthermore, H_2O_2 catalyzes the synthesis of salicylic acid by mobilizing the activity of benzoic acid 2-hydroxylase enzyme triggering the systemic acquired responses and inducing expression of pathogenesis-related genes (Leon et al. 1995; Kuzniak and Urbanek, 2012).

NO triggers the activity of defense genes

Another signaling molecule, NO is also involved in regulating jasmonic acid signaling through de-nitrosylation and nitrosylation of tyrosine residues triggering hypersensitive responses. Some studies stated that NO is involved in changing the configuration of non-expressor of pathogenesis related gene-1 (NPR1). NPR1 is considered as a key transcriptional co-regulator involved in stimulating plant defense responses by the S-nitrosylation of cysteine-156 residue in plants (Tada et al. 2008; Mukhtar et al. 2009; Kovacs et al. 2015). Adhikari et al. (2019) reported induction in the expression of allene oxide synthase (AOS) and 12-oxophytodienoate reductase-1 (OPR1) involved in jasmonic acid biosynthesis pathway in the tomato seedlings treated with plasma-activated water. In addition to the activation of plant immune responses, NO was suggested to play a significant role in controlling the survival and virulence of several fungal pathogens in plants (Arasimowicz-Jelonek and Floryszak-Wieczorek, 2016). Supporting this, Perez et al. (2019) reported a lack of antimicrobial activity against *Xanthomonas campestris* that could be related to the absence of ONOOH, NO_2^- species and extremely low concentrations of H_2O_2 generated during plasma treatment.

These studies suggest that crop plants respond to various stresses by instigating several morphological, biochemical and molecular mechanisms by robust cross-talks among various signaling pathways (Nejat and Mantri, 2017). All these different mechanisms are interdependent and consecutively promote hypersensitive responses either by programmed cell death or necrosis, leading to microbial inactivation or enhancing the capability of plants in alleviating diseases through the expression of various defense response genes. Nevertheless, the specific mechanisms that lead to virus inactivation by non-thermal plasma remain unclear. Few studies demonstrated that exposure of viruses to non-thermal plasma often results in modification or degradation of viral proteins along with nucleic acids and lipids in the enveloped viruses (Davies, 2003; Morgan et al. 2004; Cadet et al. 2008; Tanaka et al. 2014). Yet, few research groups identified that damage to viral coat protein itself is adequate for deactivating viral particles with their genetic material remaining intact after non-thermal plasma treatment (Yasuda et al. 2010; Zimmermann et al. 2011; Filipić et al. 2019).

Although a majority of signaling mechanisms cited above were due to the activity of reactive oxygen and nitrogen species generated from sources other than plasma, they are presumed to perform similar activities in non-thermal plasma-treated plants. Supporting this notion, few studies have demonstrated that exogenous application of reactive oxygen and nitrogen species as well as ultra-violet radiation could impose similar effects resulting in enhanced stress resistance, before stress events (Antoniou et al. 2016; Thomas and Puthur 2017). Hence, future research should be essentially centered on mechanisms promoting plant disease control by non-thermal plasma treatment to clear up various existing hypotheses and a precise understanding of technology. Regardless of the overall complexity, we propose a general scheme (Fig. 3) with hypothetical illustration of the mechanisms involved in microbial inactivation and activation of plant defense responses.

Non-thermal plasma to enhance plant tolerance to abiotic stresses

Abiotic stress remains a major issue faced by agriculture. Several abiotic stress conditions such as drought, heat, cold, salinity and heavy metal toxicity often affect the plant growth resulting in poor crop stand and reduced agricultural productivity (Soltani et al. 2006; Jabbari et al. 2013). Based

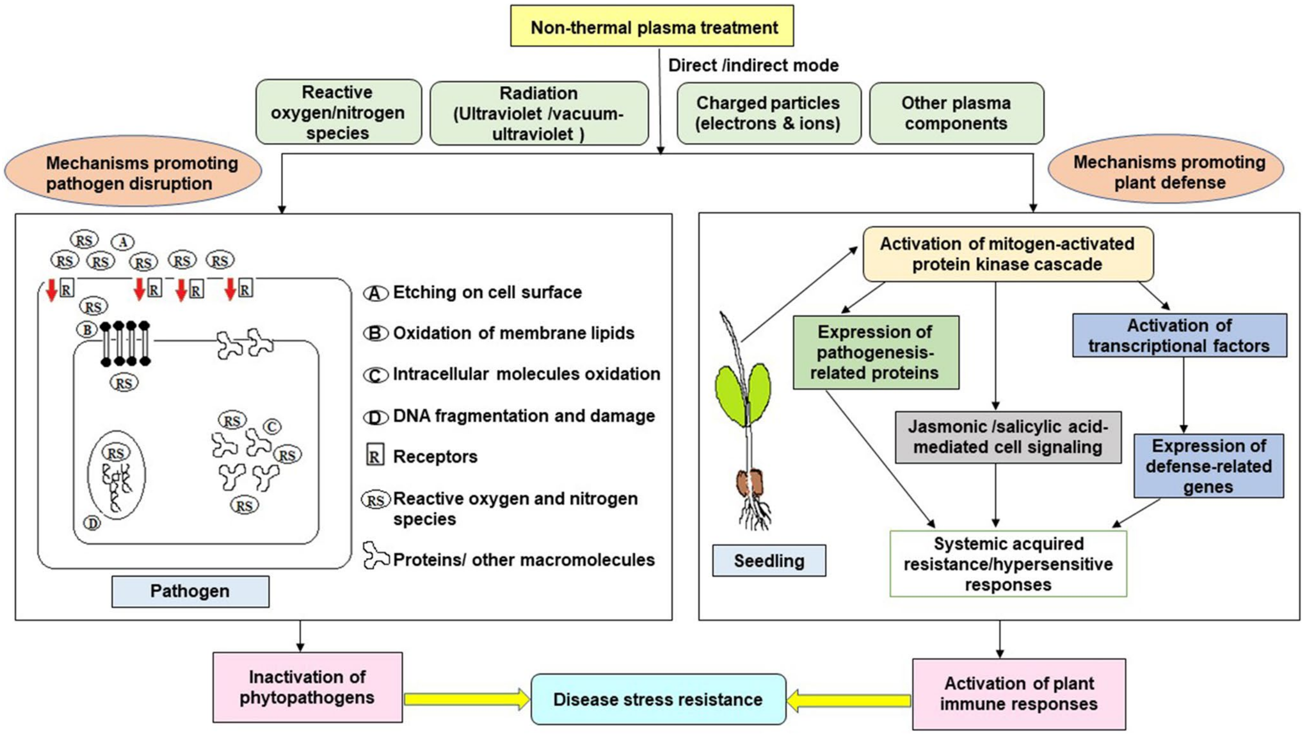

Fig. 3 Putative mechanisms enhancing microbial inactivation and disease stress tolerance in plants through non-thermal plasma treatment. Plasma components initially act to prevent entry of pathogen into the plant cell by etching, degradation of vital proteins and DNA in the cells of microbes. If the pathogen subsides this damage and gain entry into the plant cells, plasma components could possibly trigger defense responses mainly by the activity of reactive species. Reactive species such as NO and H_2O_2 act as key signaling molecules in triggering mitogen-activated protein kinase cascade resulting in transcription and activation of defense-related genes. Besides they tend to provoke secondary defense signaling pathways mediated by phytohormones and expression of pathogenesis-related proteins. Altogether, these processes would facilitate systemic acquired resistance/hypersensitive responses in plants leading to programmed cell death or necrosis in the infected tissues

on the FAO reports, Cramer et al. (2011) stated that approximately 96.5% of global rural land area is affected by abiotic stresses. Boyer (1982) during early 1980s, reported that as much as 70% of crop production loses may occur due to environmental factors alone. Dhlamini et al. (2005) reported that 6-20% of crop production costing around US$120 billion is estimated to be lost, due to the effect of various abiotic stress factors world-wide annually.

Recently, using genetic and biotechnological tools breeders have generated varieties that are resilient to various climatic stress conditions. However, practical use of stress tolerant varieties have their own limitations similar to disease resistant varieties. On the other hand, non-genetic approaches include conventional practices such as exogenous application of hormones, plant growth regulators, metabolites (Hsu et al. 2003; Ma et al. 2004; Huang et al. 2013; Yang et al. 2014; Godoy et al. 2021) and treatment using magnetic and electric fields (Javed et al. 2011; He et al. 2016). Among these methods, application of non-thermal plasma has captured attention in recent years as an environmentally safe and sustainable approach of seed treatment for the management of abiotic stresses in plants.

Non-thermal plasma treatment on seeds is anticipated to act as a "mild stressor" that could induce signaling pathways and strengthen the plant to combat other abiotic stress factors. Supporting this idea, research conducted to assess the role of non-thermal plasma treatment in the alleviation of abiotic stresses demonstrated multiple positive effects of plasma treatment over the conventional technologies (Wu et al. 2007; Ling et al. 2015; Guo et al. 2017; Iranbakhsh et al. 2017; de Groot et al. 2018; Kabir et al. 2019).

Drought stress tolerance

Drought or water-deficit stress is a major climatic stress that reduces crop production and food security. Approximately 454 million hectares of area across the world experienced drought-induced yield losses accounting to US$166 billion during 1983-2009 (Kim et al. 2019). Under drought stress conditions, treatment with non-thermal plasma was identified to provoke a broad spectrum of physiological and developmental process in plants that are discussed in detail in this section.

Plasma treatment promotes seedling growth, activities of superoxide dismutase and peroxidase and increase proline concentration in wheat under drought stress (Huang, 2010). In another study, Guo et al. (2017) simulated drought stress on wheat plants using polyethylene glycol. The seeds treated with dielectric barrier discharge plasma could alleviate polyethylene glycol-induced drought stress, whereas untreated seedlings were prone to oxidative damage due to increase in H_2O_2, O_2^- and malonaldehyde concentrations. Further, significant enhancement in the cellular abscisic acid levels, superoxide dismutase and catalase activity was noticed in the treated plants. In addition, plasma could induce the expression of late embryogenesis abundant (LEA) proteins, as well as the regulatory genes, sucrose non-fermenting-1-related protein kinases-2 (SnRK2) and pyrroline-5 carboxylate synthase (P5CS) enhancing tolerance to drought stress.

In oilseed rape, *Brassica napus* L., effects of plasma treatment were analyzed by imposing drought stress, and seeds of both drought-sensitive and drought-tolerant cultivars were exposed to cold plasma. Interestingly, treated seeds of both cultivars had lesser oxidative damage and normal metabolism due to enhanced production of antioxidants, viz., superoxide dismutase and catalase. Further, accumulation of compatible osmolytes was also reported in the treated seedlings promoting osmotic balance under stress condition (Ling et al. 2015). Similarly, Adhikari et al. (2020a) evaluated the effect of plasma priming on the tomato seeds artificially imposed to polyethylene glycol-induced drought stress. Treatment with plasma could induce seed germination and seedling growth under drought stress mediated by the activity of phytohormones, antioxidants, stress signaling genes and histone modifications.

Tolerance against heavy metal toxicity

Severe anthropogenic activities including mineral extraction and excess use of inorganic fertilizers and pesticides generally result in heavy metal pollution. Accumulation of toxic heavy metals in the soil could affect seed germination and vital developmental processes of plants reducing growth, yield and quality (FAO 2015; Manzoor et al. 2018). In wheat, a study was conducted to investigate the role of plasma in limiting heavy metal phytotoxicity, using low pressure dielectric barrier discharge generated from argon/air and argon/oxygen. Both plasma variants could interfere with the expression of cadmium transporter genes of wheat, viz., low-affinity cation transporter-1 (*Ta*LCT1) and heavy metal adenosine triphosphatase-2 (*Ta*HMA2) in the roots (Kabir et al. 2019). Further, cadmium-induced oxidative damage in tissues was reported to be significantly declined due to upregulated activity of wheat superoxide dismutase (*Ta*SOD) and catalase (*Ta*CAT) genes. The inhibitory effect of plasma on cadmium uptake was also ascribed to the decrease in cellular pH resulting from the activity of reactive species that severely limited the bioavailability of the metal from the rhizosphere. Along with this, reduction in electrolyte leakage, decline in cell death in roots and shoots as well as the improvement in total soluble proteins were noticed. Results from grafting experiments using plasma-treated seedlings as root stock suggested, NO to play a key role as signaling molecule in alleviating cadmium toxicity (Kabir et al. 2019).

Hou et al. (2021) investigated the effects of cold plasma treatment in limiting the uptake of cadmium and lead by water spinach. The effect of different modes of plasma treatment including treatment on seeds, plasma-activated water and both was also analyzed. Findings suggested combination of treatments to be highly effective in controlling cadmium uptake by plants, by inhibiting the expression of metal transporter genes, similar to that reported by Kabir et al. (2019). However, plasma treatment induced the concentration of lead, that could be probably assigned to the activation of lead transporter genes in roots of water spinach. The authors expressed that the inconsistency in the results with respect to lead accumulation could be due to certain limitations in their study including reduced sample size and lack of optimization of plasma parameters. These studies demonstrate that application of non-thermal plasma could open up new avenues in the field of bioremediation.

Plasma priming for protection against nanoparticles

Metal and metal oxide nanoparticles provide beneficial effects to plants, including heavy metal decontamination (Cartwright et al. 2020). However, few studies reported cytotoxic effects of nanoparticles on plant cellular systems, notably at high concentrations (Yang et al. 2015; Boonyanitipong et al. 2011). Iranbakhsh et al. (2018b) found that pre-treatment with cold plasma could induce a growth-promoting and protective effect against zinc oxide (ZnO) nanoparticles in bell pepper. They suggested that plasma compounds such as NO, ozone and ultra-violet radiation promote the activity of antioxidants, viz., phenylalanine ammonia lyase and peroxidase that alleviate the toxic effects imposed by nano-ZnO. Similarly, non-thermal plasma-treated seedlings of *Melissa officinalis* could overcome the toxic effect of high concentrations of selenium and ZnO nanoparticles (Babajani et al. 2019). Pre-treatment of *Chicorium intybus* seedlings using non-thermal plasma could mitigate the phytotoxic effects of elevated concentrations of selenium nanoparticles, and significant improvement in the growth characteristics of treated seedlings was also noticed (Abedi et al. 2020).

Salinity tolerance

Soil salinity impairs plant growth and development through osmotic stress, oxidative stress, and nutritional imbalance and exerts cytotoxic effects on plants due to excessive uptake of sodium and chloride ions (Isayenkov et al. 2012). Recently, few studies expressed the capability of non-thermal plasma treatment in ameliorating the impact of salinity stress in rice and wheat. Iranbakhsh et al. (2017) noted that dielectric barrier discharge plasma treatment on wheat seedlings could promote tolerance against salt stress. The authors observed induction in the expression of heat shock factor-4A (HSFA4A) and activity of peroxidase and phenylalanine ammonia lyase in treated seedlings, that triggered defense responses and assisted in combating the deteriorative impacts of salinity.

Sheteiwy et al. (2018) treated the seeds of rice using cold plasma, salicylic acid and a combination of both to investigate their effects on salinity tolerance. Both the treatments individually and in combination performed well, and could enhance plant growth and uptake of nutrients, besides reducing ion imbalance under salinity stress. Simultaneously, increase in the activity of enzymatic and non-enzymatic antioxidants as well as decrease in oxidative damage due to sharp decline in the concentrations of reactive oxygen species and malonaldehyde was noticed in the treated seedlings.

Alleviation of multiple stress factors

Emerging evidences suggest that pre-treatment with non-thermal plasma could elicit adaptive responses in plants to protect themselves against a combination of stress factors. When multiple stressors, viz., salinity, cold and drought, were simultaneously imposed on plasma pre-treated seeds of maize, drastic changes in osmolyte production and accumulation of proline, as well as soluble sugars were observed (Wu et al. 2007). A significant rise in the activity of peroxidase resulting in reduction in electrolyte leakage was noticed that aided in coping with the multiple stress factors. Likewise, cold plasma treatment on cotton seeds significantly improved germination and water absorption in the seedlings that were subjected to adverse climatic conditions of chilling temperature and water scarcity (de Groot et al. 2018).

Bafoil et al. (2019) studied the effect of non-thermal plasma treatment in managing salinity and osmotic stress in *Arabidopsis thaliana* mutants glabra-2 (gl2) and glycerol-3-phosphate acyltransferase-5 (gpat5). Pre-treatment with non-thermal plasma induced structural changes on the mantle layers of the seed coat reducing its permeability and improved seed germination by diminishing the negative effects of stress to a certain extent. Similarly, irrigation with plasma-activated water in barley improved tolerance against a combination of stress factors including hypoxia, low-temperature and salinity (Gierczik et al. 2020).

Stress tolerance through plasma-mediated epigenetic changes

Few studies recently demonstrated far-reaching effects of plasma treatment through epigenetic modifications. Argon plasma treatment promoted seed germination and seedling growth in soybean under oxygen-deficit conditions by modulating the demethylation of adenosine triphosphate (ATP), the target of rapamycin (TOR) and growth-regulating factor (GRF) genes involved in energy metabolism (Zhang et al. 2017). In other study, non-thermal plasma treatment has been proved to enhance the germination of rice seeds matured under heat stress. Knock-down expression of nine-cis-epoxycarotenoid dioxygenase (NCED) genes, *i.e.*, *Os*NCED2 and *Os*NCED5 involved in abscisic acid synthesis, and up-regulation of abscisic acid 8'-hydroxylase (ABA8'OH) genes, *i.e., Os*ABA8'OH-1 and *Os*ABA8'OH-3 involved in abscisic acid catabolism along with α-amylase synthesizing genes, viz*., Os*Amy1A, *Os*Amy1C, *Os*Amy3B and *Os*Amy3E was reported in this study. It was concluded that plasma treatment could provoke epigenetic changes through hypo-methylation of *Os*Amy1C and *Os*Amy3E promoters and hyper-methylation of the *Os*NCED5 promoter (Suriyasak et al. 2021). The alterations in DNA methylation patterns caused by plasma treatment could revise the gene expression and enhance germination of rice seeds that were exposed to heat stress during grain filling stage. Similarly, Adhikari et al. (2020a) noticed histone modifications in tomato seedlings subjected to cold plasma priming due to the activity of reactive oxygen species. The study observed up-regulation in the enzymatic activities of histone acetyltransferase (HAT) and histone-lysine N-methyl-transferases (HFMET), key players involved in regulating histone modifications. The convergent action of these enzymes was anticipated to regulate the activity of different biochemicals and stress-related genes that ultimately conferred drought stress tolerance.

Overall, non-thermal plasma induces several modifications at biochemical and molecular levels in plants during abiotic stress management (Table 2). The outcome from the above studies clearly epitomizes that, application of non-thermal plasma treatment in crops has the potential to enhance abiotic stress tolerance. They tend to decrease the oxidative damage to plant membranes through the promotion of both enzymatic and non-enzymatic antioxidants, and upregulate the activities of enzymes related to secondary metabolism. At the molecular level, plasma-elicited plant responses mainly comprise of triggering the activity of stress-related genes and epigenetic modifications that act in

Table 2 Published data on the effect of non-thermal plasma in provoking abiotic stress responses in various plant species

Crop	Type of plasma	Impact summary	Reference
Drought stress			
Wheat	Arc discharge plasma	Plasma treatment induced the activity of peroxidase, α-amylase and soluble proteins enhancing drought tolerance. However, the degree of tolerance varied between the cultivars	Huang (2010)
Oil seed rape	Radio frequency capacitively coupled plasma generated using helium gas	The activities of superoxide dismutase and catalase were increased by 17.71%, 16.25% and 13.0%, 13.2% in drought-sensitive and drought-tolerant cultivars, respectively. Further, enhancement in germination rate, soluble sugars and proteins as well as reduction in malonaldehyde content was noticed under water-deficit conditions	Ling et al. (2015)
Wheat	Dielectric barrier discharge plasma	Pre-treatment with plasma enhanced seedling length, proline, soluble sugars and antioxidant activity, whereas noticeable decrease in malonaldehyde content and reactive oxygen species was reported. Besides, germination potential and germination rate increased by 27.2% and 27.6%, respectively, during drought stress	Guo et al. (2017)
Tomato	Plasma-activated water	Application of plasma-activated water could upregulate the synthesis of pathogenesis-related genes, induce hormone-mediated signaling, epigenetic modifications and proline accumulation promoting both disease resistance and drought stress tolerance	Adhikari et al. (2020a)
Heavy metal stress			
Wheat	Low pressure dielectric barrier discharge using (air/argon, argon/oxygen)	Reduction in pH of seeds due to plasma-induced nitrogen species resulted in decreased bioavailability of cadmium. Increase in the activity of catalase and super oxide dismutase, total soluble protein content and down-regulation of cadmium transporter genes was noticed in treated seedlings	Kabir et al. (2019)
Water spinach	Atmospheric pressure plasma jet	Plasma treatment could significantly reduce the bioconcentration factor of cadmium from 0.864 to 0.54. However, the concentration of lead remained unaffected through plasma treatment	Hou et al. (2021)
Salinity stress			
Wheat	Dielectric barrier discharge plasma	Treatment with plasma enhanced the expression of heat shock transcription factor-4A, peroxidase activity by 25%, phenylalanine ammonia lyase activity by 21% enhancing tolerance to salt stress. Besides, increase in shoot dry mass (18%), leaf area (18%) and chlorophyll-a content (37.5%) were reported	Iranbakhsh et al. (2017)
Rice	Cold plasma treatment using nitrogen and oxygen	Reported synergistic effect of plasma treatment and salicylic acid priming in alleviating the salt stress. Noticed significant improvement in the activity of superoxide dismutase, peroxidase, catalase and ascorbate peroxidase, as well as sharp decline malonaldehyde content, reactive species and cell death	Sheteiwy et al. (2019)

Table 2 (continued)

Crop	Type of plasma	Impact summary	Reference
Multiple stress factors			
Maize	Atmospheric pressure cold plasma	Soluble sugar content, proline, peroxidase activity increased by average of 5.5%, 24.7% and 33.3%, respectively, and electrolyte leakage decreased by 20.9% resulting in tolerance against drought, cold and salinity	Wu et al. (2007)
Cotton	Cold plasma generated using air/ argon	Treatment using air for 3 min had significant impact in enhancing water absorption, whereas treatment for 21 min using air could enhance both water absorption and germination, followed by 81 min of argon plasma treatment increasing tolerance to both cold and water-deficit stress	de Groot et al. (2018)
Arabidopsis thaliana	Dielectric barrier discharge plasma using ambient air	Plasma treatment could induce modifications on the seed surface reducing its permeability and enhancing water uptake as well as germination rate in the presence of salinity and osmotic stress	Bafoil et al. (2019)
Barley	Plasma-activated water	Treatment with plasma-activated water could enhance tolerance to low-temperature stress and hypoxia. NaCl-induced salt stress was mitigated through improvement in antioxidants, cysteine, γ-glutamylcysteine and carotenoids. Together with glutathione, these compounds could scavenge excess reactive oxygen species and reduce salt-stress induced damage	Gierczik et al. (2020)
Other stress factors			
Soybean	Argon plasma	Plasma-induced alleviation of oxygen-deficit stress through epigenetic modifications including demethylation of genes involved in energy metabolism	Zhang et al. (2017)
Capsicum annum	Atmospheric pressure cold plasma	Inhibitory effects of zinc oxide nanoparticles on plants were potentially alleviated through plasma treatment. The activities of phenylalanine ammonia lyase and soluble phenols were enhanced and significant improvement in chlorophyll-a and carotenoids was noticed	Iranbakhsh et al. (2018a, b)
Melissa officinalis	Atmospheric pressure cold plasma	Toxic signs of both zinc oxide and selenium nanoparticles were partly mitigated by the activity of plasma components. Induction in peroxidase and phenylalanine ammonia lyase activity along with improvement in growth characteristics and biomass accumulation was noticed	Babajani et al. (2019)
Chicorium intybus	Dielectric barrier discharge plasma	Plasma treatment could alleviate the toxic effects of selenium nanoparticles induced by the activity of catalase and peroxidase. Further, improvement in shoot and root biomass, number of flowers and their fresh weight was noticed	Abedi et al. (2020)
Rice	Atmospheric pressure cold plasma	Plasma treatment could provoke epigenetic changes through both methylation and demethylation of promoters involved in α-amylase synthesis and abscisic acid synthesis promoting germination in seeds exposed to heat stress	Suriyasak et al. (2021)

min minutes

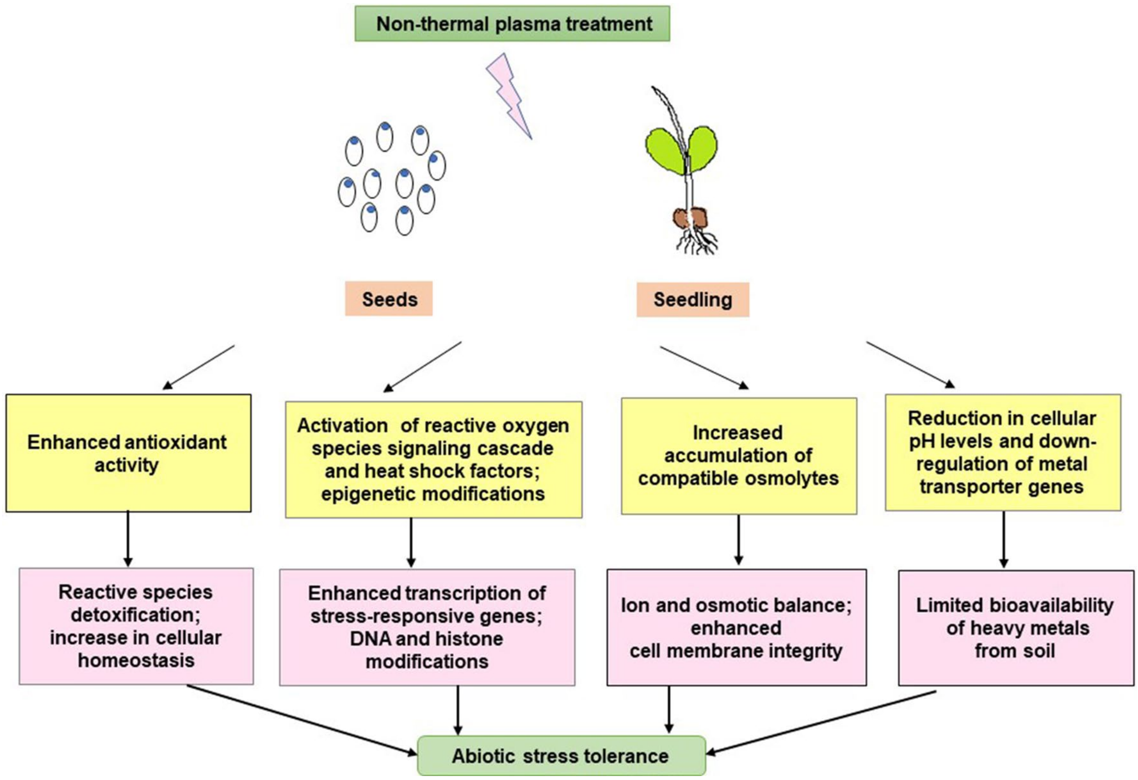

Fig. 4 Plausible non-thermal plasma elicited responses in plants against various abiotic stresses Pre-treatment of seeds or seedlings with non-thermal plasma could **i** induce synthesis of antioxidants that scavenge excess reactive species and re-establish homeostasis, **ii** activate several transcription factors that trigger the expression of stress-responsive genes and epigenetic changes lead to DNA and histone protein modifications, **iii** accumulation of soluble osmolytes helps to maintain ion and osmotic balance as well as reduce the production of malonaldehyde, **iv** reactive species produced from plasma reduce the cellular pH and knock-down the activity of metal transporter genes that impairs the uptake of heavy metals from soil (It is to be noted that effect of reduction in pH on uptake of heavy metals varies with the crop species)

a synergistic manner and assist the plants in alleviating various stress factors.

Non-thermal plasma and plant interactions favoring alleviation of abiotic stresses

Non-thermal plasma-plant interactions are complex, and thus, a plethora of responses are expected to be generated in plants by the activity of various plasma components (Fig. 4). Pre-treatment with plasma could provoke both the synthesis and activity of several antioxidants involved in maintaining reactive oxygen species homeostasis. Further plasma-elicited expression of several stress-responsive genes, transcription factors and epigenetic modifications has been reported to enhance the plant's ability to fight against several abiotic stress factors that are discussed in detail in this section.

Plasma-induced antioxidants as scavengers of reactive oxygen species

Changes in the metabolism of reactive oxygen species are critical for plant cells. Based on their concentrations, reactive oxygen species can feature either beneficial or damaging effects to plant cells. Generally, overproduction of reactive oxygen species during stress results in deficiency of antioxidant enzymes leading to toxic events in cells. It is hypothesized that plasma-generated reactive species could also add to the cellular production level of endogenous reactive oxygen and nitrogen species. Thus, high level of oxidative stress could be detrimental to cell survival and in many cases lead to induction of apoptosis. Nevertheless, experimental evidences strongly suggest that plasma treatment with a low power and short exposure time could strengthen cellular antioxidant systems and regulate crop stress tolerance without imposing any kind of oxidative stress.

Several researchers opined that synthesis and activity of various antioxidants, e.g. superoxide dismutase, peroxidase, catalase, phenylalanine ammonia lyase and dehydrogenase, could be enhanced by pre-treatment of seeds and seedlings using non-thermal plasma under environmentally controlled conditions (Wu et al. 2007; Ling et al. 2015; Guo et al. 2017; Iranbakhsh et al. 2017, 2018a, b; de Groot et al. 2018; Kabir et al. 2019). This ensures prevention of oxidative damage and scavenging of excess reactive species improving survival of plants under stress condition. Among various antioxidants, peroxidase and phenylalanine ammonia lyase were deciphered to play a crucial rule during both biotic and abiotic stresses (Iranbakhsh et al. 2018a, b). Iranbakhsh et al. (2017) reported induction in the activity of peroxidase due to the elevation of HSFA4A, and through signaling mediated by bioactive components of plasma. Many researchers opined that increase in the activity of peroxidase could contribute to tolerance against various abiotic stress factors in different crop species (Wu et al. 2007; Iranbakhsh et al. 2017; Babajani et al. 2019). Similarly, a close association between activity of phenylalanine ammonia lyase and defense-related responses has been observed in plants (Valifard et al. 2014). Since non-thermal plasma treatment could intensify the activity of these two key antioxidants, it is anticipated to enhance abiotic stress tolerance in treated plants.

On the other side, secondary metabolites synthesized in plants, especially phenols and anthocyanins, also function as powerful non-enzymatic antioxidants mediating reactive oxygen species scavenging, and are widely reported to be involved in stress protection (Šamec et al. 2021). In agreement to this, application of non-thermal plasma on seeds of *Echinacea purpurea* demonstrated a remarkable increase in the concentrations of vitamin-C and other polyphenols, that eventually augmented radical scavenging activity (Mildaziene et al. 2018). Bußler et al. (2015) witnessed increase in the concentration of flavonoid glycosides through dielectric barrier discharge treatment in peas that enhanced tolerance to oxidative stress. Besides enhancing abiotic stress tolerance, the anthocyanins and phenols synthesized in response to non-thermal plasma treatment were known to instigate the disease stress tolerance in maize (Filatova et al. 2020). Phenylalanine ammonia lyase is considered as a key enzyme involved in polyphenol biosynthesis and is transcriptionally regulated by various environmental and developmental factors (Rossi et al. 2016). It can critically influence the defense responses in plants for a wide range of abiotic stresses (Wada et al. 2014). A positive relation between the activity of phenylalanine ammonia lyase and intensification of phenolic compounds involved in plant cell wall strengthening was noticed, resulting in osmotic stress tolerance in few crop species (Dehghan et al. 2014; Rossi et al. 2016).

Osmotic adjustment is another vital mechanism adopted by plants wherein different osmolytes *i.e.,* proline, soluble sugars, glycine betaine and other inorganic ions, assemble in the cells to manage drought stress. Accumulation of these osmolytes promotes water uptake and maintenance of cell membrane integrity during water scarcity (Ashraf and Foolad, 2007; Talbi et al. 2015). Plasma technology is known to improve osmolyte production during stress condition (Wu et al. 2007; Ling et al. 2015; Guo et al. 2017). In addition, accumulation of proline at high concentrations in plant cells under stress has been identified to enhance the reactive oxygen species scavenging capacity and combat oxidative damage (Filatova et al. 2020).

Plasma-generated reactive species for stress signaling

In plants, the below-ground trait popularly known as root system architecture often plays a prominent role in management of several abiotic stress factors. Root traits are known to exhibit plasticity and respond to external environmental stimuli including soil moisture, nutrients, temperature, pH and microbial communities (Comas et al. 2013). Fernández-Marcos et al. (2011) reported prominent role of reactive nitrogen species NO (generated from three NO donors) to play a key role in influencing root system as a part of drought adaptation strategy in plants. The alterations in the root morphology were ascribed to the hormonal balance especially auxin concentration in meristems of primary roots mediated via post-transcriptional activity of peptidyl-prolyl cis-/transisomerase-1 (PIN1) protein involved in auxin transport. Few studies observed significant alterations in the root system in the non-thermal plasma-treated seedlings (Guo et al. 2017; Iranbakhsh et al. 2018a, b; Abedi et al. 2020), but pertinent role of plasma generated NO in altering root the architecture has not been discussed.

Recently, a study revealed that non-thermal plasma treatment in tomato could alleviate polyethylene glycol-induced drought stress through the signal transduction mediated by plasma-generated NO and H_2O_2 (Adhikari et al. 2020a). The prominent role of NO and H_2O_2 as cellular signaling molecules to overcome salinity in non-thermal plasma-treated barley seeds has been discussed by Gierczik et al. (2020). Sheteiwy et al. (2019) noticed enhanced growth and differentiation in plasma-treated rice seedlings exposed to salinity stress, due to the signaling mediated by plasma components especially O_3, NO and ultra-violet radiation. It has been hypothesized that various reactive oxygen and nitrogen species along with radiation generated from plasma could act as endogenous signaling molecules (Iranbakhsh et al. 2018a). They tend to form an integrated signaling network that could affect and regulate numerous physiological processes (Mittler et al. 2004; Wojtyla et al. 2016).

Iranbakhsh et al. (2018a) reported that NO produced from plasma could activate the mitogen-activated protein kinase cascade that is involved in inducing the expression of defense-related genes. Along with this, NO was reported as a key signaling molecule involved in hampering heavy metal uptake by plants (Kabir et al. 2019). It is a well-established fact that pH surrounding the rhizosphere of plants could influence availability of minerals and nutrients (Dong et al. 2008). Concurrent to this, Kabir et al. (2019) reported that NO generated from non-thermal plasma could induce acidification and decrease pH on the surface of treated seeds, that subsequently affected the plant's capacity to uptake cadmium metal from soil. Nevertheless, it is important to note that the effect of pH on cadmium uptake is expected to vary among different species of crops.

Plasma-induced expression of stress-related genes

The biological processes and cell interactions taking part during plant stress management are recognized as highly complex. The stress responses of plants are controlled by multiple signaling pathways and overlaps tend to exist between the patterns of gene expression that are induced in plants, in reaction to different stresses. The stress-responsive genes play a critical role in cellular protection, synthesis of functional proteins, regulation of signal transduction and gene expression patterns during stress condition (Valifard et al. 2014). The induction of stress-responsive genes occurs primarily at the level of transcription and coordinated by regulatory network of several transcription factors. Broadly, heat shock factors are considered as essential transcription factors that regulate genes affecting plant growth and development. In agreement to this, promising role of different heat shock factors in modifying the expression of various stress-responsive genes in the non-thermal plasma-treated seedlings has been reported. The activation of various heat shock factors through non-thermal plasma treatment promoted heavy metal tolerance (cadmium) in wheat and rice (Shim et al. 2009), drought tolerance in Arabidopsis (Yoshida et al. 2008) and salinity tolerance in wheat (Iranbakhsh et al. 2017). Indeed, HSFA4A acts as a substrate for mitogen-activated protein kinase-3/6 (MPK3/MPK6), and activates the mitogen-activated protein kinase pathway. This, in turn, leads to the transcriptional activation of several stress-related genes involved in conferring tolerance to various abiotic stresses (Pérez-Salamó et al. 2014; Smékalová et al. 2014). Besides, mitogen-activated protein kinase is also identified to play a decisive role in coordinating the activity of various other transcription factors including WRKY, MYB and ZAT, that in turn, accompany the transcription of a large set of target genes (Pérez-Salamó et al. 2014).

In akin to the activity of stress-responsive genes, epigenetic modifications play an important role in imparting tolerance against climate extremes. In the recent past, few studies demonstrated capability of non-thermal plasma treatment in facilitating epigenetic modifications on the treated targets, by inducing DNA and histone modifications (Adhikari et al. 2020a; Zhang et al. 2017; Suriyasak et al. 2021). Application of cold plasma on the rice seeds exposed to high temperature stress during grain filling stage could alter the DNA methylation patterns of the promoter regions of genes involved in abscisic acid metabolism and α-amylase synthesis modifying the corresponding gene expression (Suriyasak et al. 2021). Similarly, plasma treatment on seeds of soybean induced selective demethylation of ATP genes (ATP a1, ATP b1), TOR and GRF genes (GRF-5, GRF-6) involved in metabolic processes. This selective DNA demethylation patterns probably enhanced the expression of these genes that displayed growth provoking effects enhancing seed germination and sprout growth of soybean under conditions of hypoxic environment (Zhang et al. 2017). Along with DNA methylation and demethylation processes, another element of epigenetic regulation includes histone modification. Adhikari et al. (2020a) observed upregulation in the activity of histone modifying enzymes HAT and HFMET. Both the enzymes are reported as key players involved in the acetylation of lysine residues, and methylation of lysine and arginine residues of histones, respectively (Pikaard and Scheid 2014). The integrated activity of HAT and HFMET was found to be responsible for modulating the expression of antioxidants, phytohormones, and stress-responsive genes enhancing drought stress tolerance (Adhikari et al. 2020a).

Although a majority of the studies were emphasized on identifying the capability of non-thermal plasma treatment in controlling abiotic stress factors, cardinal mechanisms or pathways promoting stress management at the molecular level, viz., signal transduction and epigenetic gene regulation, were not deeply investigated and remain ambiguous. Besides many studies reported prominent role of few reactive species (NO and H_2O_2) during abiotic stress management, whereas pertinent role of other plasma-generated components, i.e., radiation and charged particles, has not been properly examined. Hence, more convincing studies are required particularly at molecular level to understand the principal mechanisms implicated in the plant-plasma interactions during abiotic stress management, for precise understanding of the technology.

Conclusion

Non-thermal plasma research has made significant leaps in several fields; however, pertinent to agriculture, it is in its infancy stage. Intrinsic to enhancing agricultural productivity, beyond doubt, the technology has been exploited largely for enhancing seed germination and successfully geared up in food processing industry. Its level of insight in addressing the critical issues in agriculture, especially in terms of stress tolerance, is still lacking and restricted to laboratory conditions. So far, most of the research focussed on identifying the impacts of non-thermal plasma treatment in managing various stress conditions in plants. Whereas, the underlying molecular processes cardinal to the stress management were not clearly elucidated yet and exclusive efforts need to be dissipated in this direction. Of late, many studies reported the effects of non-thermal plasma treatment in regulating various diseases and abiotic stresses in plants independently, that rarely exist in natural ecosystems. Since investigating stress factors in isolation does not construe the effects of more than one kind of stress on plants, future studies should concentrate to discern the plant-plasma interactions in response to multiple stresses. Thus, identifying key regulators elicited by non-thermal plasma treatment that converge both disease control and abiotic stress response pathways are fundamental and create new avenues for wide scale adaptation of technology.

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