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

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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

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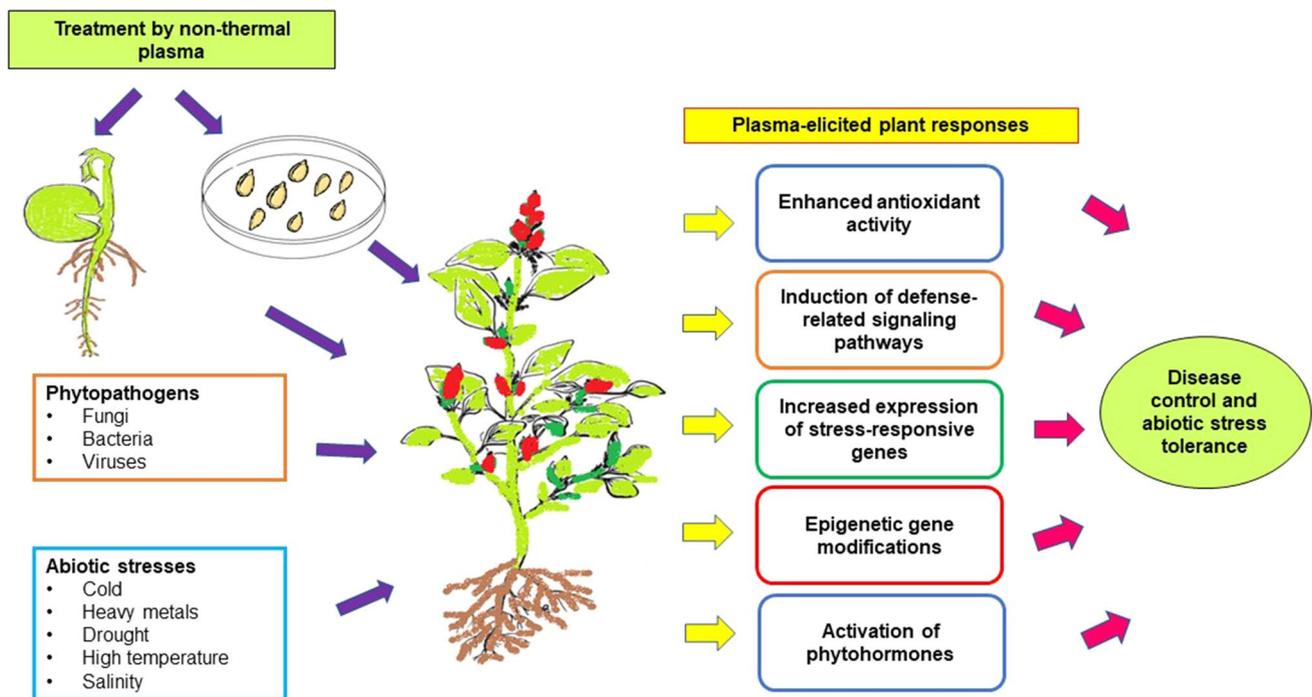
produced at either low pressure or atmospheric pressure, which facilitates plasma use in agriculture, food processing, water decontamination and medicine (Ambrico et al. 2020; Babajani et al. 2019; Pérez-Pizá et al. 2021; Puač et al. 2018, Surowsky et al. 2015, Zhang et al. 2018, von Woedtke et al. 2013).

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). Pre-treatment 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 activ-

ity 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; Stijns 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 losses 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                |
|--|--|---|---|--------------------------|
| <i>Fungal diseases</i>                   |  |   |   |                          |
| <i>Philodendron erubescens</i> leaves    | Atmospheric cold plasma jet using helium/oxygen                  | <i>Colletotrichum gloeosporioides</i>   | 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 | <i>Aspergillus</i> sp. and <i>Penicillium</i> 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         | <i>Aschocyta pinodella</i> and <i>Fusarium culmorum</i>   | 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         | <i>Fusarium</i> sp., <i>Alternaria</i> sp., <i>Penicillium</i> sp., <i>Cladosporium</i> sp., <i>Colletotrichum gloeosporioides</i> , <i>Mucor</i> sp. and <i>Kabatiella caulivora</i> | 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   | <i>Fusarium graminearum</i> , <i>Fusarium oxysporum</i> and <i>Neurospora crassa</i>  | 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         | <i>Gibberella fujikuroi</i>   | 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                                  | <i>Cladosporium fulvum</i>  | Significant reduction in the rotting of infected seeds due to degradation of fungal protein and DNA   | Lu et al. (2014)         |
| Brassicaceous seeds                      | Both atmospheric pressure and low pressure plasma                | <i>Rhizoctonia solani</i>   | 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        | <i>Fusarium oxysporum</i> f. sp. <i>lycopersici</i>   | Significant reduction in spore germination percent after 10 min of treatment  | Panngom et al. (2014)    |
| Barley and corn seeds                    | Glow discharge plasma  | <i>Aspergillus</i> sp., <i>Penicillium</i> sp. and <i>Fusarium</i> 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   | <i>Fusarium fujikuroi</i>   | 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   | <i>Alternaria</i> sp., <i>Fusarium</i> sp., <i>Gibberella</i> sp., <i>Penicillium</i> sp., <i>Rhizopus stolonifera</i> , <i>Trichoderma</i> 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  | <i>Aspergillus flavus</i> and <i>Aspergillus parasiticus</i>  | A significant reduction in the inoculum load of both the fungi <i>A. flavus</i> and <i>A. parasiticus</i> 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  | Khamseen et al. (2016)   |
| Wheat seeds               | DCSBD plasma   | <i>Fusarium</i> sp., <i>Tricothecium roseum</i> and <i>Aspergillus</i> 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  | <i>Fusarium fujikuroi</i>   | 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   | <i>Cladosporium cucumerinum</i> and <i>Didymella bryoniae</i>   | Treatment for 20 s in cucumber could completely eradicate spores of <i>Cladosporium</i> sp., whereas 60-80% reduction in spores of <i>Didymella</i> sp. was noticed. In pepper, 50-80% reduction in the spores of <i>Didymella</i> 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 | <i>Diaporthe/Phomopsis</i> complex  | Reversal of oxidative damage caused by fungal complex in the treated seeds was noticed  | Pérez Pizá et al. (2018) |
| Pine seeds                | DCSBD plasma   | <i>Fusarium circinatum</i>  | 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                          | <i>Colletotrichum gloeosporioides</i>   | 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   | <i>Aspergillus flavus</i> ,<br><i>Aspergillus alternata</i> and<br><i>Fusarium culmorum</i> | Reduction in colonies of <i>F. culmorum</i> by 3.79-log after 60 s of treatment was noticed; while <i>A. flavus</i> and <i>A. alternata</i> 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    | <i>Diaporthe longicolla</i>   | Plasma-induced lipid peroxidation and antioxidant activity severely affected the growth of fungal colonies  | Pérez-Pizá et al. (2021) |
| <i>Bacterial diseases</i>                    |  |   |   |                          |
| Suspension culture                           | Gliding arc discharge plasma                             | <i>Erwinia caratovora</i>   | Reported glid-arc discharge to be more effective in killing bacterial colonies without lag time   | Moreau et al. (2007)     |
| Tomato seeds                                 | Inductive Helium plasma                                  | <i>Ralstonia solanacearum</i>   | 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   | <i>Clavibacter michiganensis</i> subsp. <i>michiganensis</i> and <i>Erwinia amylovora</i>   | 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 | <i>Geobacillus stearothermophilus</i>   | 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                          | <i>Xanthomonas campestris</i>   | 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)   |
| Hydrophobic solution                         | Discharge plasma reactor                                 | <i>Ralstonia solanacearum</i>   | Reported significant reduction in the bacterial spore density from 10 <sup>7</sup> to 10 <sup>2</sup> 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                                     | <i>Burkholderia plantarii</i>  | Disease severity index reduced to 38.6% in the treated seeds   | Ochi et al. (2017)     |
| Suspension culture        | Roller conveyer atmospheric pressure plasma                         | <i>Xanthomonas campestris</i> pv. <i>campestris</i>  | Viable bacterial cells decreased exponentially from $5.0 \times 10^8$ to $9.8 \times 10^5$ 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   | <i>Clavibacter</i> sp., <i>Dickeya solani</i> , <i>Xanthomonas</i> sp. and <i>Pectobacterium</i> sp. | Treatment with plasma induced complete destruction of three bacterial species; while partial reduction in colonies of <i>Pectobacterium</i> sp. was noticed          | Motyka et al. (2018)   |
| <i>Viral diseases</i>     |   |  |  |                        |
| 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, $\Phi$ 174 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).

Pannong 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 peroxy-nitrite 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<sub>2</sub>O<sub>2</sub>) 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 phyto-bacterial 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 conveyor, 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,  $\beta$ -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; Niedźwiedz 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 ( $^1\text{H}$ ) and demonstrated that  $^1\text{H}$  surrounded by water molecules, *i.e.*,  $\text{H}(\text{H}_2\text{O})_m$ , played a key role in the deactivation of air-borne microbes, probably due to its long life.  $\text{H}(\text{H}_2\text{O})_m$  released from the device reacted with oxygen ( $\text{O}_2$ ) and superoxide anion ( $\text{O}_2^-$ ) surrounded by  $(\text{H}_2\text{O}_2)_n$ , generating highly reactive secondary species such as hydroperoxyl radical ( $\text{HO}_2$ ) and dioxidanide ( $\text{HO}_2^-$ ), 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  $\text{H}_2\text{O}_2$ ) 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

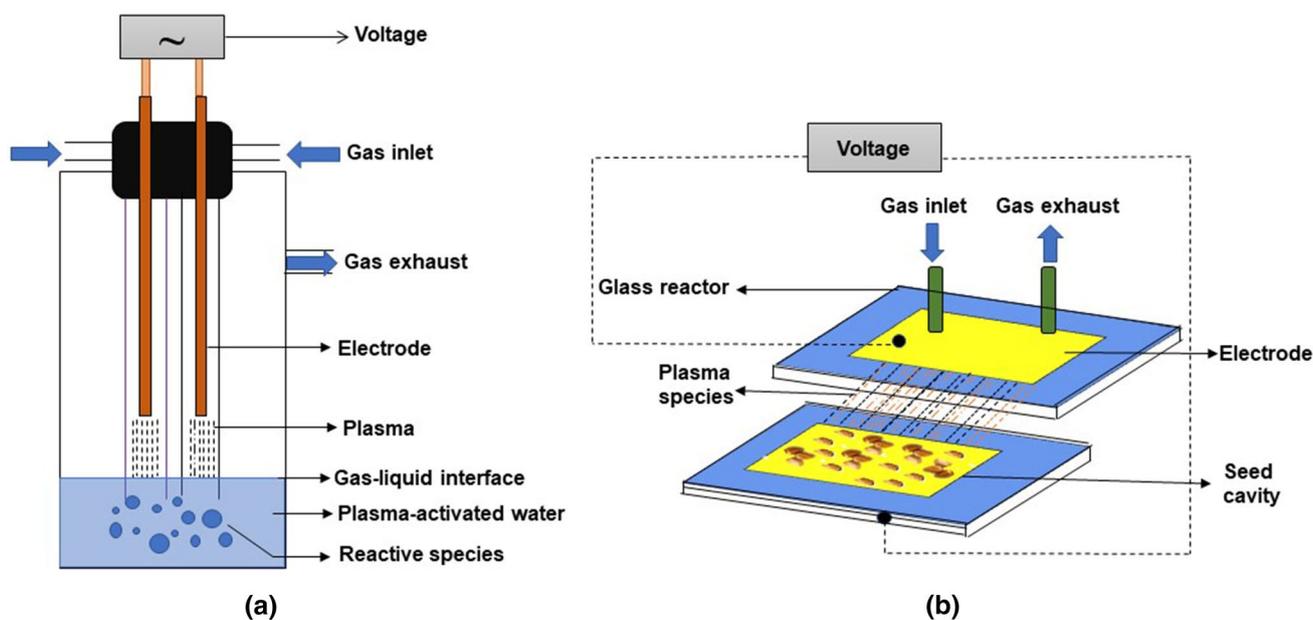
The microbicidal efficiency of ultra-violet radiation on any biological material largely depends on the dose delivered

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 (Laroussi 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 metastable, 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

2014; Pannngom 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<sub>3</sub>), singlet oxygen (<sup>1</sup>O<sub>2</sub>), hydroxyl radical (•OH), superoxide radical (O<sub>2</sub><sup>•-</sup>), nitric oxide (•NO/NO), peroxy nitrates (ONOO<sup>-</sup> and OONOO<sup>-</sup>), H<sub>2</sub>O<sub>2</sub>, nitrites and nitrates (NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup>).

The primary reactive oxygen and nitrogen species such as •OH, NO, H<sub>2</sub>O<sub>2</sub>, O and O<sub>3</sub> 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; Pannngom 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

plasma or indirectly by placing the seeds at a sufficient distance from the plasma. (Adopted and re-drawn from Sivachandiran and Khacef 2017)

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<sub>3</sub>, H<sub>2</sub>O<sub>2</sub>, NO<sub>2</sub><sup>-</sup> and NO<sub>3</sub><sup>-</sup>, and secondary reactive species (Pannngom 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, •NO, •OH and O<sub>2</sub><sup>•-</sup>, non-radical chemical compounds such as singlet oxygen (<sup>1</sup>O<sub>2</sub>), 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., •OH, in exerting bactericidal effects, versus long-lived species, e.g., H<sub>2</sub>O<sub>2</sub>. Among various by-products generated, peroxy nitrates (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  $\text{H}_2\text{O}_2$ ,  $\text{O}_2^{\bullet-}$ ,  $^1\text{O}_2$  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; Pawlat et al. 2018).

Lipid peroxidation also induces the production of intermediate reactive compounds such as peroxy, 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 (Niedźwiedz 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,  $\text{H}_2\text{O}_2$  and oxides of nitrogen ( $\text{NO}_x$ ) generated from plasma should follow similar mechanisms of action as exogenously applied  $\text{H}_2\text{O}_2$  and  $\text{NO}_x$  and thus should have a similar impact on plant cells (Antoniou et al. 2016; Thomas and Puthur, 2017).

### **$\text{H}_2\text{O}_2$ -mediated signaling and regulation of transcription factors**

In general, unstable reactive oxygen species including  $\text{O}_2^{\bullet-}$  and  $^1\text{O}_2$  might react with various components of plant cells. Stable reactive oxygen and nitrogen species such as  $\text{H}_2\text{O}_2$  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.  $\text{H}_2\text{O}_2$  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,  $\text{H}_2\text{O}_2$  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<sub>2</sub>O<sub>2</sub> 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<sub>2</sub>O<sub>2</sub> signaling, which in turn regulate the expression of defense-related genes (Petrov and Van Breusegem, 2012). Furthermore, H<sub>2</sub>O<sub>2</sub> 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

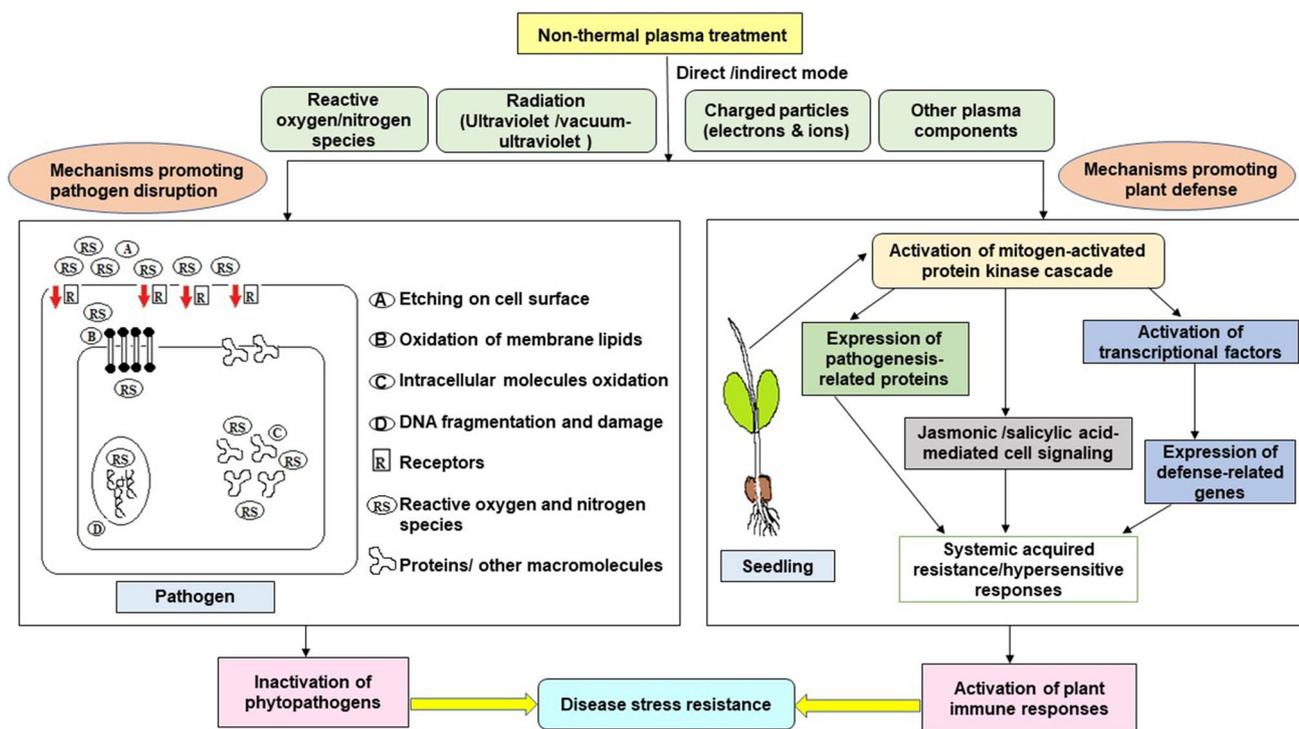
of antimicrobial activity against *Xanthomonas campestris* that could be related to the absence of ONOOH, NO<sub>2</sub><sup>-</sup> species and extremely low concentrations of H<sub>2</sub>O<sub>2</sub> generated during plasma treatment.

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<sub>2</sub>O<sub>2</sub> act as key signaling mol-

ecules 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 losses 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 (*TaLCT1*) and heavy metal adenosine triphosphatase-2 (*TaHMA2*) 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 (*TaSOD*) and catalase (*TaCAT*) 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., *OsNCED2* and *OsNCED5* involved in abscisic acid synthesis, and up-regulation of abscisic acid 8'-hydroxylase (ABA8'OH) genes, i.e., *OsABA8'OH-1* and *OsABA8'OH-3* involved in abscisic acid catabolism along with  $\alpha$ -amylase synthesizing genes, viz., *OsAmy1A*, *OsAmy1C*, *OsAmy3B* and *OsAmy3E* was reported in this study. It was concluded that plasma treatment could provoke epigenetic changes through hypo-methylation of *OsAmy1C* and *OsAmy3E* promoters and hyper-methylation of the *OsNCED5* 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

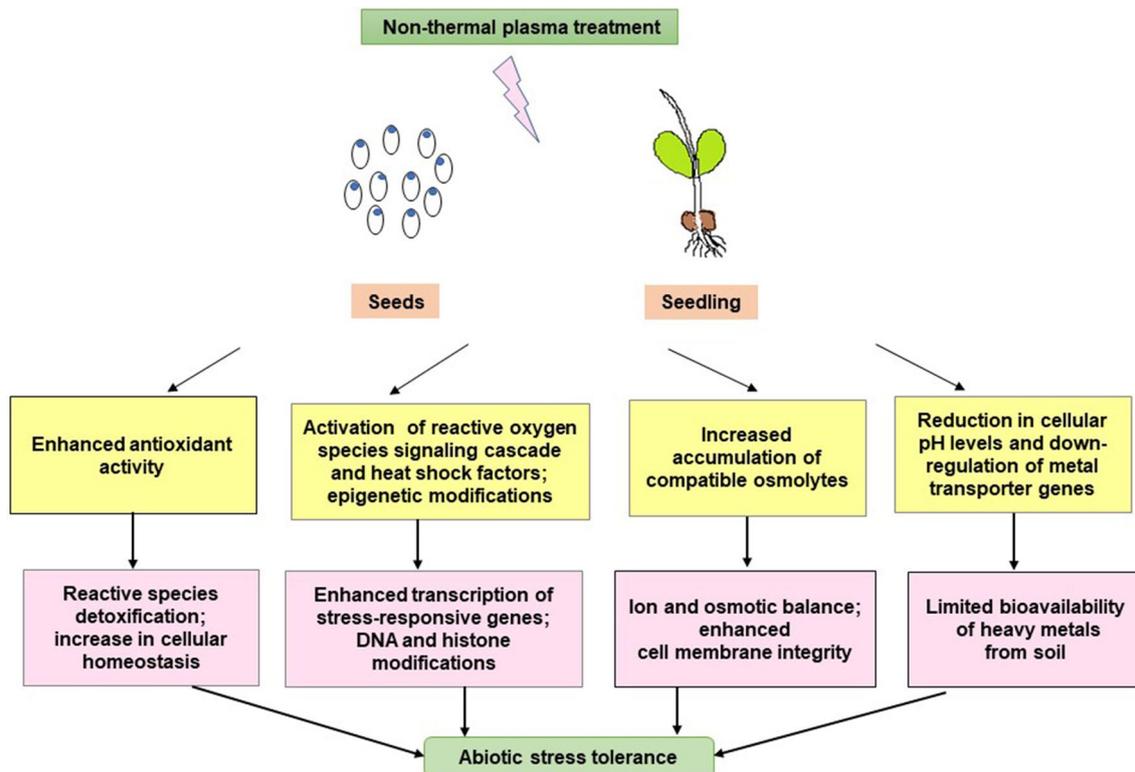
**Table 2** Published data on the effect of non-thermal plasma in provoking abiotic stress responses in various plant species

| Crop                      | Type of plasma  | Impact summary  | Reference                |
|---------------------------|---|---|--------------------------|
| <i>Drought stress</i>     |   |   |                          |
| Wheat                     | Arc discharge plasma  | Plasma treatment induced the activity of peroxidase, $\alpha$ -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)  |
| <i>Heavy metal stress</i> |   |   |                          |
| 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)        |
| <i>Salinity stress</i>    |   |   |                          |
| 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                    |
|--------------------------------|---|---|------------------------------|
| <i>Multiple stress factors</i> |   |   |                              |
| 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)       |
| <i>Arabidopsis thaliana</i>    | 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, $\gamma$ -glutamylcysteine and carotenoids. Together with glutathione, these compounds could scavenge excess reactive oxygen species and reduce salt-stress induced damage | Gierczik et al. (2020)       |
| <i>Other stress factors</i>    |   |   |                              |
| 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)          |
| <i>Capsicum annum</i>          | 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) |
| <i>Melissa officinalis</i>     | 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)       |
| <i>Chicorium intybus</i>       | 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 $\alpha$ -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 role 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-/trans-isomerase-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<sub>2</sub>O<sub>2</sub> (Adhikari et al. 2020a). The prominent role of NO and H<sub>2</sub>O<sub>2</sub> 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<sub>3</sub>, 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; Wojtyła 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  $\alpha$ -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 up-regulation 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<sub>2</sub>O<sub>2</sub>) 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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## References

- Abedi S, Iranbakhsh A, Ardebili ZO, Ebadi M (2020) Seed priming with cold plasma improved early growth, flowering, and protection of *Cichorium intybus* against selenium nanoparticle. *J Theor Appl Phys* 14(2):113–119. <https://doi.org/10.1007/s40094-020-00371-8>
- Adhikari B, Adhikari M, Ghimire B, Park G, Choi EH (2019) Cold atmospheric plasma-activated water irrigation induces defense hormone and gene expression in tomato seedlings. *Sci Rep* 9(1):16080. <https://doi.org/10.1038/s41598-019-52646-z>
- Adhikari B, Adhikari M, Ghimire B, Adhikari BC, Park G, Choi EH (2020a) Cold plasma seed priming modulates growth, redox homeostasis and stress response by inducing reactive species in tomato (*Solanum lycopersicum*). *Free Radical Bio Med* 156:57–69. <https://doi.org/10.1016/j.freeradbiomed.2020.06.003>
- Adhikari B, Pangomm K, Veerana M, Mitra S, Park G (2020b) Plant disease control by non-thermal atmospheric-pressure plasma. *Front Plant Sci* 11:77. <https://doi.org/10.3389/fpls.2020.00077>
- Agathokleous E, Calabrese EJ (2019) Hormesis: the dose response for the 21st century: The future has arrived. *Toxicology* 425:152249
- Agathokleous E, Kitao M, Calabrese EJ (2019) Hormesis: a compelling platform for sophisticated plant science. *Trends Plant Sci* 24(4):318–327. <https://doi.org/10.1016/j.tplants.2019.01.004>
- Ambrico PF, Šimek M, Morano M, Angelini RMDM, Minafra A, Trotti P, Ambrico M, Prukner V, Faretra F (2017) Reduction of microbial contamination and improvement of germination of sweet basil (*Ocimum basilicum* L.) seeds via surface dielectric barrier discharge. *J Phys D Appl Phys* 50(30):305401. <https://doi.org/10.1088/1361-6463/aa77c8>
- Ambrico PF, Šimek M, Rotolo C, Morano M, Minafra A, Ambrico M, Pollastro S, Gerin D, Faretra F, Angelini RMDM (2020) Surface dielectric barrier discharge plasma: a suitable measure against fungal plant pathogens. *Sci Rep* 10(1):3673. <https://doi.org/10.1038/s41598-020-60461-0>
- Antoniou C, Savvides A, Christou A, Fotopoulos V (2016) Unravelling chemical priming machinery in plants: the role of reactive oxygen-nitrogen-sulfur species in abiotic stress tolerance enhancement. *Curr Opin Plant Sci* 33:101–107. <https://doi.org/10.1016/j.cpb.2016.06.020>
- Arasimowicz-Jelonek M, Floryszak-Wieczorek J (2016) Nitric oxide in the offensive strategy of fungal and oomycete plant pathogens. *Front Plant Sci* 7:252. <https://doi.org/10.3389/fpls.2016.00252>
- Ashraf M, Foolad MR (2007) Roles of glycine betaine and proline in improving plant abiotic stress resistance. *Environ Exp Bot* 59(2):206–216. <https://doi.org/10.1016/j.envexpbot.2005.12.006>
- Assaraf MP, Ginzburg C, Katan J (2002) Weakening and delayed mortality of *Fusarium oxysporum* by heat treatment: flow cytometry and growth studies. *Phytopathology* 92(9):956–963. <https://doi.org/10.1094/PHYTO.2002.92.9.956>
- Avramidis G, Stüwe B, Wascher R, Bellmann M, Wieneke S, von Tiedemann A, Viöl W (2010) Fungicidal effects of an atmospheric pressure gas discharge and degradation mechanisms. *Surf Coat Technol* 205:S405–S408. <https://doi.org/10.1016/j.surfcoat.2010.08.141>
- Babajani A, Iranbakhsh A, Ardebili ZO, Eslami B (2019) Seed priming with non-thermal plasma modified plant reactions to selenium or zinc oxide nanoparticles: cold plasma as a novel emerging tool for plant science. *Plasma Chem Plasma Process* 39(1):21–34. <https://doi.org/10.1007/s11090-018-9934-y>
- Bafoil M, Ru AL, Merbahi N, Eichwad O, Dunand C, Yousfi M (2019) New insights of low-temperature plasma effects on germination of three genotypes of *Arabidopsis thaliana* seeds under osmotic and saline stresses. *Sci Rep* 9(1):8649. <https://doi.org/10.1038/s41598-019-44927-4>
- Bakshi M, Oelmüller R (2014) WRKY transcription factors: Jack of many trades in plants. *Plant Signal Behav* 9(2):e27700. <https://doi.org/10.4161/psb.27700>
- Bermúdez-Aguirre D, Wemlinger E, Pedrow P, Barbosa-Cánovas G, García-Pérez M (2013) Effect of atmospheric pressure cold plasma (APCP) on the inactivation of *Escherichia coli* in fresh produce. *Food Control* 34(1):149–157. <https://doi.org/10.1016/j.foodcont.2013.04.022>
- Bertaccini A, Biondi E, Canel A, Colombo V, Contaldo N, Gherardi M (2017) Plasma activated water to enhance plant defences. In: Proceedings of the 23rd international symposium on plasma chemistry, p 206
- Birmingham JG (2004) Mechanisms of bacterial spore deactivation using ambient pressure nonthermal discharges. *IEEE Trans*

- Plasma Sci 32(4):1526–1531. <https://doi.org/10.1109/TPS.2004.832609>
- Boonyanitipong P, Kositsup B, Kumar P, Baruah S, Dutta J (2011) Toxicity of ZnO and TiO<sub>2</sub> nanoparticles on germinating rice seed *Oryza sativa* L. *Int J Biosci Biochem Bioinform* 1(4):282
- Boudam MK, Moisan M, Saoudi B, Popovici C, Gherardi N, Massines F (2006) Bacterial spore inactivation by atmospheric-pressure plasmas in the presence or absence of UV photons as obtained with the same gas mixture. *J Phys D Appl Phys* 39(16):3494–3507. <https://doi.org/10.1088/0022-3727/39/16/S07>
- Bourke P, Ziuzina D, Boehm D, Cullen PJ, Keener K (2018) The potential of cold plasma for safe and sustainable food production. *Trends Biotechnol* 36(6):615–626. <https://doi.org/10.1016/j.tibtech.2017.11.001>
- Boyer JS (1982) Plant productivity and environment. *Science* 218(4571):443–448. <https://doi.org/10.1126/science.218.4571.443>
- Brasoveanu M, Nemtanu M, Surdu-Bob C, Karaca G, Erper I (2015) Effect of glow discharge plasma on germination and fungal load of some cereal seeds. *Rom Rep Phys* 67(2):617–624
- Brickner PW, Vincent RL, First M, Nardell E, Murray M, Kaufman W (2003) The application of ultraviolet germicidal irradiation to control transmission of air-borne disease: bioterrorism countermeasure. *Public Health Rep* 118(2):99–114
- Bußler S, Herppich WB, Neugart S, Schreiner M, Ehlbeck J, Rohn S, Schlüter O (2015) Impact of cold atmospheric pressure plasma on physiology and flavonol glycoside profile of peas (*Pisum sativum* ‘Salamanca’). *Food Res Int* 76:132–141. <https://doi.org/10.1016/j.foodres.2015.03.045>
- Butscher D, Zimmermann D, Schuppler M, Rohr RV (2016) Plasma inactivation of bacterial endospores on wheat grains and polymeric model substrates in a dielectric barrier discharge. *Food Control* 60:636–645. <https://doi.org/10.1016/j.foodcont.2015.09.003>
- Cadet J, Douki T, Ravanat J-L (2008) Oxidatively generated damage to the guanine moiety of DNA: mechanistic aspects and formation in cells. *Acc Chem Res* 41(8):1075–1083. <https://doi.org/10.1021/ar700245e>
- Cartwright A, Jackson K, Morgan C, Anderson A, Britt DW (2020) A review of metal and metal-oxide nanoparticle coating technologies to inhibit agglomeration and increase bioactivity for agricultural applications. *Agronomy* 10(7):1018. <https://doi.org/10.3390/agronomy10071018>
- Challinor AJ, Watson J, Lobell DB, Howden SM, Smith DR, Chhetri N (2014) A meta-analysis of crop yield under climate change and adaptation. *Nat Clim Chang* 4(4):287–291. <https://doi.org/10.1038/nclimate2153>
- Comas L, Becker S, Cruz VM, Byrne PF, Dierig DA (2013) Root traits contributing to plant productivity under drought. *Front Plant Sci* 4:442. <https://doi.org/10.3389/fpls.2013.00442>
- Cramer GR, Urano K, Delrot S, Pezzotti M, Shinozaki K (2011) Effects of abiotic stress on plants: a systems biology perspective. *BMC Plant Biol* 11:163. <https://doi.org/10.1186/1471-2229-11-163>
- Cui D, Yin Y, Wang J, Wang Z, Ding H, Ma R, Jiao Z (2019) Research on the physio-biochemical mechanism of non-thermal plasma-regulated seed germination and early seedling development in *Arabidopsis*. *Front Plant Sci* 10:1322. <https://doi.org/10.3389/fpls.2019.01322>
- Dasan BG, Mutlu M, Boyaci IH (2016) Decontamination of *Aspergillus flavus* and *Aspergillus parasiticus* spores on hazelnuts via atmospheric pressure fluidized bed plasma reactor. *Int J Food Microbiol* 216:50–59. <https://doi.org/10.1016/j.ijfoodmicro.2015.09.006>
- Davies MJ (2003) Singlet oxygen-mediated damage to proteins and its consequences. *Biochem Biophys Res Commun* 305(3):761–770. [https://doi.org/10.1016/S0006-291X\(03\)00817-9](https://doi.org/10.1016/S0006-291X(03)00817-9)
- De Geyter N, Morent R (2012) Nonthermal plasma sterilization of living and nonliving surfaces. *Annu Rev Biomed Eng* 14:255–274
- de Groot GJB, Hundt A, Murphy AB, Bange MP, Mai-Prochnow A (2018) Cold plasma treatment for cotton seed germination improvement. *Sci Rep* 8(1):14372. <https://doi.org/10.1038/s41598-018-32692-9>
- Dehghan S, Sadeghi M, Pöppel A, Fischer R, Lakes-Harlan R, Kavousi HR, Vilcinskas A, Rahnamaeian M (2014) Differential inductions of phenylalanine ammonia-lyase and chalcone synthase during wounding, salicylic acid treatment, and salinity stress in safflower, *Carthamus tinctorius*. *Biosci Rep* 34:e00114. <https://doi.org/10.1042/BSR20140026>
- Del Rio D, Stewart AJ, Pellegrini N (2005) A review of recent studies on malondialdehyde as toxic molecule and biological marker of oxidative stress. *Nutr Metab Cardiovasc Dis* 15(4):316–328. <https://doi.org/10.1016/j.numecd.2005.05.003>
- Deng X, Shi J, Kong MG (2006) Physical mechanisms of inactivation of *Bacillus subtilis* spores using cold atmospheric plasmas. *IEEE Trans Plasma Sci* 34(4):1310–1316. <https://doi.org/10.1109/TPS.2006.877739>
- Deora A, Gossen BD, Walley F, McDonald MR (2011) Boron reduces development of clubroot in canola. *Can J Plant Pathol* 33(4):475–484. <https://doi.org/10.1080/07060661.2011.620630>
- Dhananjayan V, Jayakumar S, Ravichandran B (2020) Conventional methods of pesticide application in agricultural field and fate of the pesticides in the environment and human health. In: Thomas RKR, Volova T, Jayachandran K (eds) *Controlled release of pesticides for sustainable agriculture*. Springer, Berlin, pp 1–39. [https://doi.org/10.1007/978-3-030-23396-9\\_1](https://doi.org/10.1007/978-3-030-23396-9_1)
- Dhlamini Z, Spillane C, Moss JP, Ruane J, Urquia N, Sonnino, A (2005) Status of research and application of crop biotechnologies in developing countries: preliminary assessment. *FAO* 1–53. <https://www.fao.org/3/y5800e/Y5800E00.htm>
- Dietz K-J, Mittler R, Noctor G (2016) Recent progress in understanding the role of reactive oxygen species in plant cell signaling. *Plant Physiol* 171(3):1535–1539. <https://doi.org/10.1104/pp.16.00938>
- Dobrynin D, Fridman G, Friedman G, Fridman A (2009) Physical and biological mechanisms of direct plasma interaction with living tissue. *New J Phys* 11(11):115020. <https://doi.org/10.1088/1367-2630/11/11/115020>
- Dong J, Mao WH, Zhang GP, Wu FB, Cai Y (2008) Root excretion and plant tolerance to cadmium toxicity—a review. *Plant Soil Environ* 53(5):193–200. <https://doi.org/10.17221/2205-PSE>
- Dzimitrowicz A, Motyka A, Jamroz P, Lojkowska E, Babinska W, Terefinko D, Pohl P, Sledz W (2018) Application of silver nanostructures synthesized by cold atmospheric pressure plasma for inactivation of bacterial phytopathogens from the genera *Dickeya* and *Pectobacterium*. *Mater* 11(3):331. <https://doi.org/10.3390/ma11030331>
- Esposito G, Campa A, Pinto M, Simone G, Tabocchini MA, Belli M (2011) Adaptive response: modelling and experimental studies. *Radiat Prot Dosim* 143(2–4):320–324. <https://doi.org/10.1093/rpd/ncq474>
- FAO (2015) *Status of the World’s Soil Resources: Main Report*. FAO, ITPS; Rome, Italy
- FAO (2019) *New standards to curb the global spread of plant pests and diseases*. <https://www.fao.org/news/story/en/item/1187738/icode/>. Accessed on 19 December, 2021
- Fernández-Marcos M, Sanz L, Lewis DR, Muday GK, Lorenzo O (2011) Nitric oxide causes root apical meristem defects and growth inhibition while reducing PIN-FORMED 1 (PIN1)-dependent acropetal auxin transport. *Proc Natl Acad Sci* 108(45):18506–18511. <https://doi.org/10.1073/pnas.1108644108>

- Filatova I, Azharonok V, Kadyrov M, Beljavsky V, Gvozдов A, Shik A, Antonuk A (2011) The effect of plasma treatment of seeds of some grain and legumes on their sowing quality and productivity. *Rom J Phys* 56:139–143
- Filatova I, Lyushkevich V, Goncharik S, Zhukovsky A, Krupenko N, Kalatskaja J (2020) The effect of low-pressure plasma treatment of seeds on the plant resistance to pathogens and crop yields. *J Phys D Appl Phys* 53(24):244001. <https://doi.org/10.1088/1361-6463/ab7960>
- Filipić A, Primc G, Zaplotnik R, Mehle N, Gutierrez-Aguirre I, Ravnikar M, Mozetič M, Žel J, Dobnik D (2019) cold atmospheric plasma as a novel method for inactivation of potato virus Y in water samples. *Food Environ Virol* 11(3):220–228. <https://doi.org/10.1007/s12560-019-09388-y>
- Filipić A, Gutierrez-Aguirre I, Primc G, Mozetič M, Dobnik D (2020) Cold Plasma, a new hope in the field of virus inactivation. *Trends Biotechnol* 38(11):1278–1291. <https://doi.org/10.1016/j.tibtech.2020.04.003>
- Fridman A (2008) Plasma biology and plasma medicine. In: Plasma chemistry. Cambridge University Press, New York, pp 848–961
- Gay-Mimbrera J, García MC, Isla-Tejera B, Rodero-Serrano A, García-Nieto AV, Ruano J (2016) Clinical and biological principles of cold atmospheric plasma application in skin cancer. *Adv Ther* 33(6):894–909. <https://doi.org/10.1007/s12325-016-0338-1>
- Ghesquière B, Jonckheere V, Colaert N, Van Durme J, Timmerman E, Goethals M, Schymkowitz J, Rousseau F, Vandekerckhove J, Gevaert K (2011) Redox proteomics of protein-bound methionine oxidation. *Mol Cell Proteom* 10(5):M110.006866. <https://doi.org/10.1074/mcp.M110.006866>
- Gierczik K, Vukušić T, Kovács L, Székely A, Szalai G, Milošević S, Kocsy G, Kutasi K, Galiba G (2020) Plasma-activated water to improve the stress tolerance of barley. *Plasma Process Polym* 17(3):1900123. <https://doi.org/10.1002/ppap.201900123>
- Godoy F, Olivos-Hernández K, Stange C, Handford M (2021) Abiotic stress in crop species: improving tolerance by applying plant metabolites. *Plants* 10(2):186. <https://doi.org/10.3390/plants10020186>
- Gorbanev Y, Privat-Maldonado A, Bogaerts A (2018) Analysis of short-lived reactive species in plasma–air–water systems: the dos and the do nots. *Analy Chem* 93(8):3666–3670. <https://doi.org/10.1021/acs.analchem.0c04906>
- Guo Q, Wang Y, Zhang H, Qu G, Wang T, Sun Q, Liang D (2017) Alleviation of adverse effects of drought stress on wheat seed germination using atmospheric dielectric barrier discharge plasma treatment. *Sci Rep* 7(1):1–14. <https://doi.org/10.1038/s41598-017-16944-8>
- Guo L, Xu R, Gou L, Liu Z, Zhao Y, Liu D, Zhang L, Chen H, Kong MG (2018) Mechanism of virus inactivation by cold atmospheric-pressure plasma and plasma-activated water. *Appl Environ Microbiol* 84(17):e00726–e818. <https://doi.org/10.1128/AEM.00726-18>
- Gupta A, Kumar R (2020) Management of seed-borne diseases: an integrated approach. *Seed-Borne diseases of agricultural crops: detection, diagnosis and management*. Springer, Singapore, pp 717–745
- Hahn M (2014) The rising threat of fungicide resistance in plant pathogenic fungi: Botrytis as a case study. *J Chem Biol* 7(4):133–141. <https://doi.org/10.1007/s12154-014-0113-1>
- Han L, Patil S, Boehm D, Milosavljević V, Cullen PJ, Bourke P (2016) Mechanisms of inactivation by high-voltage atmospheric cold plasma differ for *Escherichia coli* and *Staphylococcus aureus*. *Appl Environ Microbiol* 82(2):450–458. <https://doi.org/10.1128/AEM.02660-15>
- Hanbal SE, Takashima K, Miyashita S, Ando S, Ito K, Elsharkawy MM, Kaneko T, Takahashi H (2018) Atmospheric-pressure plasma irradiation can disrupt tobacco mosaic virus particles and RNAs to inactivate their infectivity. *Arch Virol* 163(10):2835–2840. <https://doi.org/10.1007/s00705-018-3909-4>
- Hashizume H, Ohta T, Takeda K, Ishikawa K, Horii M, Ito M (2014) Quantitative clarification of inactivation mechanism of *Penicillium digitatum* spores treated with neutral oxygen radicals. *Jpn J Appl Phys* 54(1S):0105. <https://doi.org/10.7567/JJAP.54.01AG05>
- He Y, Li Y, Cui L, Xie L, Zheng C, Zhou G, Zhou J, Xie X (2016) Phytochrome B negatively affects cold tolerance by regulating OsDREB1 gene expression through phytochrome interacting factor-like protein OsPIL16 in rice. *Front Plant Sci* 7:1963. <https://doi.org/10.3389/fpls.2016.01963>
- Heil M, Hilpert A, Kaiser W, Linsenmair KE (2000) Reduced growth and seed set following chemical induction of pathogen defence: Does systemic acquired resistance (SAR) incur allocation costs? *J Ecol* 88(4):645–654. <https://doi.org/10.1046/j.1365-2745.2000.00479.x>
- Heimpel GE, Mills NJ (2017) Biological control: ecology and applications. Cambridge University Press. <https://doi.org/10.1017/9781139029117>
- Heise M, Neff W, Franken O, Muranyi P, Wunderlich J (2004) Sterilization of polymer foils with dielectric barrier discharges at atmospheric pressure. *Plasma Process Polym* 9(1):23–33. <https://doi.org/10.1023/B:PAP0.0000039814.70172.c0>
- Hertwig C, Meneses N, Mathys A (2018) Cold atmospheric pressure plasma and low energy electron beam as alternative nonthermal decontamination technologies for dry food surfaces: a review. *Trends Food Sci Technol* 77:131–142. <https://doi.org/10.1016/j.tifs.2018.05.011>
- Hilker M, Schwachtje J, Baier M, Balazadeh S, Bäurle I, Geiselhardt S, Hinch DK, Kunze R, Mueller-Roerber B, Rillig MC et al (2016) Priming and memory of stress responses in organisms lacking a nervous system: priming and memory of stress responses. *Biol Rev* 91:1118–1133
- Holubová L, Kyzek S, Ďurovcová I, Fabová J, Horváthová E, Ševčovičová A, Gálová E (2020) Non-thermal plasma—a new green priming agent for plants? *Int J Mol Sci* 21(24):9466. <https://doi.org/10.3390/ijms21249466>
- Homa K, Barney WP, Davis WP, Guerrero D, Berger MJ, Lopez JL, Wyenandt CA, Simon JE (2021) Cold plasma treatment strategies for the control of *Fusarium oxysporum* f. sp. basilici in sweet basil. *HortScience* 56(1):42–51. <https://doi.org/10.21273/HORTSCI15338-20>
- Horst RK (2001) Plant diseases and their pathogens. In: Horst RK (ed) Westcott's plant disease handbook. Springer, Boston, pp 86–515
- Hosseinzadeh Colagar A, Memariani H, Sohbatazadeh F, Valinataj Omran A (2013) Nonthermal atmospheric argon plasma jet effects on *Escherichia coli* biomacromolecules. *Biotechnol Appl Biochem* 171(7):1617–1629. <https://doi.org/10.1007/s12010-013-0430-9>
- Hou CY, Kong TK, Lin CM, Chen HL (2021) The effects of plasma-activated water on heavy metals accumulation in water spinach. *Appl Sci* 11(11):5304. <https://doi.org/10.3390/app11115304>
- Hsu CC, Chen CL, Chen JJ, Sung JM (2003) Accelerated aging-enhanced lipid peroxidation in bitter melon seeds and effects of priming and hot water soaking treatments. *Sci Hortic* 98(3):201–212. [https://doi.org/10.1016/S0304-4238\(03\)00002-5](https://doi.org/10.1016/S0304-4238(03)00002-5)
- Huang MJ (2010) Physiological effect of plasma on wheat seed germination. *J Shanxi Agri Sci* 38:22–25
- Huang X, Liu Y, Li J, Xiong X, Chen Y, Yin X, Feng D (2013) The response of mulberry trees after seedling hardening to summer drought in the hydro-fluctuation belt of three gorges reservoir areas. *Environ Sci Pollut Res* 20(10):7103–7111. <https://doi.org/10.1007/s11356-012-1395-x>

- Huot B, Yao J, Montgomery BL, He SY (2014) Growth–defense tradeoffs in plants: a balancing act to optimize fitness. *Mol Plant* 7(8):1267–1287. <https://doi.org/10.1093/mp/ssu049>
- Iranbakhsh A, Ghoranneviss M, Ardebili Z, Ardebili N, Tackallou S, Nikmaram H (2017) Non-thermal plasma modified growth and physiology in *Triticum aestivum* via generated signalling molecules and UV radiation. *Biol Plant* 61(4):702–708. <https://doi.org/10.1007/s10535-016-0699-y>
- Iranbakhsh A, Ardebili NO, Ardebili ZO, Shafaati M, Ghoranneviss M (2018a) Non-thermal plasma induced expression of heat shock factor A4A and improved wheat (*Triticum aestivum* L.) growth and resistance against salt stress. *Plasma Chem Plasma Process* 38(1):29–44. <https://doi.org/10.1007/s11090-017-9861-3>
- Iranbakhsh A, Ardebili ZO, Ardebili NO, Ghoranneviss M, Safari N (2018b) Cold plasma relieved toxicity signs of nano zinc oxide in *Capsicum annuum* cayenne via modifying growth, differentiation, and physiology. *Acta Physiol Plant* 40(8):1–11. <https://doi.org/10.1007/s11738-018-2730-8>
- Isayenkov SV (2012) Physiological and molecular aspects of salt stress in plants. *Cytol Genet* 46:302–318. <https://doi.org/10.3103/S0095452712050040>
- Iseki S, Hashizume H, Jia F, Takeda K, Ishikawa K, Ohta T, Ito M, Hori M (2011) Inactivation of *Penicillium digitatum* spores by a high-density ground-state atomic oxygen-radical source employing an atmospheric-pressure plasma. *Appl Phys Express* 4(11):116201. <https://doi.org/10.1143/APEX.4.116201>
- Jabbari H, Akbari GA, Sima NAKK, Rad SAH, Alahdadi I, Hamed A, Shariatpanahi ME (2013) Relationships between seedling establishment and soil moisture content for winter and spring rapeseed genotypes. *Ind Crops Prod* 49:177–187. <https://doi.org/10.1016/j.indcrop.2013.04.036>
- Jang JY, Rhee JY, Chung GC, Kang H (2012) Aquaporin as a membrane transporter of hydrogen peroxide in plant response to stresses. *Plant Signal Behav* 7(9):1180–1181. <https://doi.org/10.4161/psb.21178>
- Javed N, Ashraf M, Akram NA, Al-Qurainy F (2011) Alleviation of adverse effects of drought stress on growth and some potential physiological attributes in maize (*Zea mays* L.) by seed electromagnetic treatment. *Photochem Photobiol* 87(6):1354–1362. <https://doi.org/10.1111/j.1751-1097.2011.00990.x>
- Jensen MK, Kjaersgaard T, Nielsen MM, Galberg P, Petersen K, O’Shea C, Skriver K (2010) The *Arabidopsis thaliana* NAC transcription factor family: structure-function relationships and determinants of ANAC019 stress signalling. *Biochem J* 426(2):183–196. <https://doi.org/10.1042/BJ20091234>
- Ji SH, Kim JS, Lee CH, Seo HS, Chun SC, Oh J, Choi EH, Park G (2019) Enhancement of vitality and activity of a plant growth-promoting bacteria (PGPB) by atmospheric pressure non-thermal plasma. *Sci Rep* 9:1044. <https://doi.org/10.1038/s41598-018-38026-z>
- Jiang J, Lu Y, Li J, Li L, He X, Shao H, Dong Y (2014) Effect of seed treatment by cold plasma on the resistance of tomato to *Ralstonia solanacearum* (Bacterial Wilt). *PLoS ONE* 9(5):e97753. <https://doi.org/10.1371/journal.pone.0097753>
- Jo Y-K, Cho J, Tsai T-C, Staack D, Kang M-H, Roh J-H, Shin D-B, Cromwell W, Gross D (2014) A non-thermal plasma seed treatment method for management of a seed-borne fungal pathogen on rice seed. *Crop Sci* 54(2):796–803. <https://doi.org/10.2135/cropsci2013.05.0331>
- Jørgensen LN, van den Bosch F, Oliver RP, Heick TM, Paveley ND (2017) Targeting fungicide inputs according to need. *Annu Rev Phytopathol* 55(1):181–203. <https://doi.org/10.1146/annurev-phyto-080516-035357>
- Joshi SG, Cooper M, Yost A, Paff M, Ercan UK, Fridman G, Fridman G, Fridman A, Brooks AD (2011) Nonthermal dielectric-barrier discharge plasma-induced inactivation involves oxidative DNA damage and membrane lipid peroxidation in *Escherichia coli*. *Antimicrob Agents Chemother* 55(3):1053–1062. <https://doi.org/10.1128/AAC.01002-10>
- Kabir AH, Rahman MM, Das U, Sarkar U, Roy NC, Reza MA, Talukder MR, Uddin MA (2019) Reduction of cadmium toxicity in wheat through plasma technology. *PLoS ONE* 14(4):e0214509. <https://doi.org/10.1371/journal.pone.0214509>
- Kang MH, Pengkit A, Choi K, Jeon SS, Choi HW, Shin DB, Choi EH, Uhm HS, Park G (2015) Differential inactivation of fungal spores in water and on seeds by ozone and arc discharge plasma. *PLoS ONE* 10(9):e0139263. <https://doi.org/10.1371/journal.pone.0139263>
- Kang M-H, Veerana M, Eom S, Uhm H-S, Ryu S, Park G (2020) Plasma mediated disinfection of rice seeds in water and air. *J Phys D Appl Phys* 53(21):214001. <https://doi.org/10.1088/1361-6463/ab79de>
- Kaushik N, Lee SJ, Choi TG, Baik KY, Uhm HS, Kim CH, Kaushik NK, Choi EH (2015) Non-thermal plasma with 2-deoxy-D-glucose synergistically induces cell death by targeting glycolysis in blood cancer cells. *Sci Rep* 5(1):8726. <https://doi.org/10.1038/srep08726>
- Khamsen N, Onwimol D, Teerakawanich N, Dechanupaprittha S, Kanokbannakorn W, Hongesombut K, Srisonphan S (2016) Rice (*Oryza sativa* L.) seed sterilization and germination enhancement via atmospheric hybrid nonthermal discharge plasma. *ACS Appl Mater Interfaces* 8(30):19268–19275. <https://doi.org/10.1021/acsami.6b04555>
- Kim J-W, Puligundla P, Mok C (2017) Effect of corona discharge plasma jet on surface-borne microorganisms and sprouting of broccoli seeds. *J Sci Food Agric* 97(1):128–134. <https://doi.org/10.1002/jsfa.7698>
- Kim W, Iizumi T, Nishimori M (2019) Global patterns of crop production losses associated with droughts from 1983 to 2009. *J Appl Meteorol Climatol* 58(6):1233–1244. <https://doi.org/10.1175/JAMC-D-18-0174.1>
- Klämpfl TG, Isbary G, Shimizu T, Li Y-F, Zimmermann JL, Stolz W, Schlegel J, Morfill GE, Schmidt H-U (2012) Cold atmospheric air plasma sterilization against spores and other microorganisms of clinical interest. *Appl Environ Microbiol* 78(15):5077–5082. <https://doi.org/10.1128/AEM.00583-12>
- Kovacs I, Durner J, Lindermayr C (2015) Crosstalk between nitric oxide and glutathione is required for Nonexpressor of Pathogenesis-Related Genes 1 (NPR1)-dependent defense signaling in *Arabidopsis thaliana*. *New Phytol* 208(3):860–872. <https://doi.org/10.1111/nph.13502>
- Kowalski W (2009) Ultraviolet germicidal irradiation handbook. Springer, Berlin
- Kumar SPJ, Prasad SR, Banerjee R, Thammineni C (2015) Seed birth to death: dual functions of reactive oxygen species in seed physiology. *Ann Bot* 116:663–668
- Kumar SPJ, Chintagunta AD, Reddy YM, Rajjou L, Garlapati VK, Agarwal DK, Prasad SR, Simal-Gandara J (2021a) Implications of reactive oxygen and nitrogen species in seed physiology for sustainable crop productivity under changing climate conditions. *Curr Plant Biol* 26:100197. <https://doi.org/10.1016/j.cpb.2021.100197>
- Kumar A, Kumar SJ, Chintagunta AD, Agarwal DK, Pal G, Singh AN, Simal-Gandara J (2021b) Biocontrol potential of *Pseudomonas stutzeri* endophyte from *Withania somnifera* (Ashwagandha) seed extract against pathogenic *Fusarium oxysporum* and *Rhizoctonia solani*. *Arch Phytopathol Pflanzenschutz* 55:1–18
- Kuzniak E, Urbanek H (2012) The involvement of hydrogen peroxide in plant responses to stresses. *Acta Physiol Plant* 22:195–203. <https://doi.org/10.1007/s11738-000-0076-4>

- Lackmann J-W, Bandow JE (2014) Inactivation of microbes and macromolecules by atmospheric-pressure plasma jets. *Appl Microbiol Biotechnol* 98(14):6205–6213. <https://doi.org/10.1007/s00253-014-5781-9>
- Laroussi M (2005) Low temperature plasma-based sterilization: overview and state-of-the-art. *Plasma Process Polym* 2(5):391–400
- Laroussi M, Leipold F (2004) Evaluation of the roles of reactive species, heat, and UV radiation in the inactivation of bacterial cells by air plasmas at atmospheric pressure. *Int J Mass Spectrom* 233:81–86. <https://doi.org/10.1016/j.ijms.2003.11.016>
- Laroussi M, Mendis DA, Rosenberg M (2003) Plasma interaction with microbes. *New J Phys* 5:41–41. <https://doi.org/10.1088/1367-2630/5/1/341>
- Lee K-Y, Joo Park B, Hee Lee D, Lee I-S, Hyun SO, Chung K-H, Park J-C (2005) Sterilization of *Escherichia coli* and MRSA using microwave-induced argon plasma at atmospheric pressure. *Surf Coat Technol* 193(1):35–38. <https://doi.org/10.1016/j.surfcoat.2004.07.034>
- Leipold F, Kusano Y, Hansen F, Jacobsen T (2010) Decontamination of a rotating cutting tool during operation by means of atmospheric pressure plasmas. *Food Control* 21(8):1194–1198. <https://doi.org/10.1016/j.foodcont.2010.02.006>
- Leon J, Lawton MA, Raskin I (1995) Hydrogen peroxide stimulates salicylic acid biosynthesis in tobacco. *Plant Physiol* 108(4):1673–1678. <https://doi.org/10.1104/pp.108.4.1673>
- Ling L, Jiangang L, Minchong S, Chunlei Z, Yuanhua D (2015) Cold plasma treatment enhances oilseed rape seed germination under drought stress. *Sci Rep* 5(1):1–10. <https://doi.org/10.1038/srep13033>
- Los A, Ziuzina D, Akkermans S, Boehm D, Cullen PJ, Impe JV, Bourke P (2018) Improving microbiological safety and quality characteristics of wheat and barley by high voltage atmospheric cold plasma closed processing. *Food Res* 106:509–521. <https://doi.org/10.1016/j.foodres.2018.01.009>
- Lu Q, Liu D, Song Y, Zhou R, Niu J (2014) Inactivation of the tomato pathogen *Cladosporium fulvum* by an atmospheric-pressure cold plasma jet. *Plasma Process Polym* 11(11):1028–1036. <https://doi.org/10.1002/ppap.201400070>
- Lu X, Naidis GV, Laroussi M, Reuter S, Graves DB, Ostrikov K (2016) Reactive species in non-equilibrium atmospheric-pressure plasmas: generation, transport, and biological effects. *Phys Rep* 630:1–84. <https://doi.org/10.1016/j.physrep.2016.03.003>
- Ma CC, Li QF, Gao YB, Xin TR (2004) Effects of silicon application on drought resistance of cucumber plants. *Soil Sci Plant Nutr* 50(5):623–632. <https://doi.org/10.1080/00380768.2004.10408520>
- Măgureanu M, Sîrbu R, Dobrin D, Gîdea M (2018) Stimulation of the germination and early growth of tomato seeds by non-thermal plasma. *Plasma Chem Plasma Process* 38(5):989–1001. <https://doi.org/10.1007/s11090-018-9916-0>
- Manzoor J, Sharma M, Wani KA (2018) Heavy metals in vegetables and their impact on the nutrient quality of vegetables: a review. *J Plant Nutr* 41:1744–1763. <https://doi.org/10.1080/01904167.2018.1462382>
- Martin SB, Dunn C, Freihaut JD, Bahnfleth WP, Lau J, Nedeljkovic-Davidovic A (2008) Ultraviolet germicidal irradiation current best practices. *Ashrae J* 50:28–36
- Mendis DA, Rosenberg M, Azam F (2000) A note on the possible electrostatic disruption of bacteria. *IEEE Trans Plasma Sci* 28(4):1304–1306. <https://doi.org/10.1109/27.893321>
- Mildaziene V, Pauzaitė G, Naucienė Z, Malakauskiene A, Zukiene R, Januskaitiene I, Jakstas V, Ivanauskas L, Filatova I, Lyushkevich V (2018) Pre-sowing seed treatment with cold plasma and electromagnetic field increases secondary metabolite content in purple coneflower (*Echinacea purpurea*) leaves. *Plasma Process Polym* 15(2):1700059. <https://doi.org/10.1002/ppap.201700059>
- Min SC, Roh SH, Niemira BA, Sites JE, Boyd G, Lacombe A (2016) Dielectric barrier discharge atmospheric cold plasma inhibits *Escherichia coli* O157:H7, *Salmonella*, *Listeria monocytogenes*, and Tulane virus in Romaine lettuce. *Int J Food Microbiol* 237:114–120. <https://doi.org/10.1016/j.ijfoodmicro.2016.08.025>
- Misra NN, Yepez X, Xu L, Keener K (2019) In-package cold plasma technologies. *J Food Eng* 244:21–31. <https://doi.org/10.1016/j.jfoodeng.2018.09.019>
- Mittler R, Vanderauwera S, Gollery M, Van Breusegem F (2004) Reactive oxygen gene network of plants. *Trends Plant Sci* 9(10):490–498. <https://doi.org/10.1016/j.tplants.2004.08.009>
- Moisan M, Barbeau J, Moreau S, Pelletier J, Tabrizian M, Yahia LH (2001) Low-temperature sterilization using gas plasmas: a review of the experiments and an analysis of the inactivation mechanisms. *Int J Pharm* 226:1–21
- Moisan M, Jean B, Marie-Charlotte C, Jacques P, Nicolas P, Bachir S (2002) Plasma sterilization. *Methods Mech Pure Appl Chem* 74:349–358
- Moreau M, Feuilloley MGJ, Veron W, Meylheuc T, Chevalier S, Brisset J-L, Orange N (2007) Gliding arc discharge in the potato pathogen *Erwinia carotovora* subsp *atroseptica*: mechanism of lethal action and effect on membrane-associated molecules. *Appl Environ Microbiol* 73(18):5904–5910. <https://doi.org/10.1128/AEM.00662-07>
- Morgan PE, Dean RT, Davies MJ (2004) Protective mechanisms against peptide and protein peroxides generated by singlet oxygen. *Free Radic Biol Med* 36(4):484–496. <https://doi.org/10.1016/j.freeradbiomed.2003.11.021>
- Motyka A, Dzimitrowicz A, Jamroz P, Lojkowska E, Sledz W, Pohl P (2018) Rapid eradication of bacterial phytopathogens by atmospheric pressure glow discharge generated in contact with a flowing liquid cathode. *Biotechnol Bioeng* 115(6):1581–1593. <https://doi.org/10.1002/bit.26565>
- Mráz I, Beran P, Šerá B, Gavril B, Hnatiuc E (2014) Effect of low-temperature plasma treatment on the growth and reproduction rate of some plant pathogenic bacteria. *Plant Pathol J* 96(1):63–67
- Mukhtar MS, Nishimura MT, Dangel J (2009) NPR1 in plant defense: It's not over 'til it's turned over. *Cell* 137(5):804–806. <https://doi.org/10.1016/j.cell.2009.05.010>
- Na YH, Park G, Choi EH, Uhm HS (2013) Effects of the physical parameters of a microwave plasma jet on the inactivation of fungal spores. *Thin Solid Films* 547:125–131. <https://doi.org/10.1016/j.tsf.2013.04.055>
- Nejat N, Mantri N (2017) Plant immune system: Crosstalk between responses to biotic and abiotic stresses the missing link in understanding plant defence. *Curr Issues Mol Biol* 1:16. <https://doi.org/10.21775/cimb.023.001>
- Nelson CL, Berger TJ (1989) Inactivation of microorganisms by oxygen gas plasma. *Curr Microbiol* 18(4):275–276. <https://doi.org/10.1007/BF01570305>
- Niedźwiedz I, Waško A, Pawłat J, Polak-Berecka M (2019) The state of research on antimicrobial activity of cold plasma. *Pol J Microbiol* 68(2):153–164. <https://doi.org/10.33073/pjm-2019-028>
- Nishioka T, Takai Y, Kawaradani M, Okada K, Tanimoto H, Misawa T, Kusakari S (2014) Seed disinfection effect of atmospheric pressure plasma and low pressure plasma on *Rhizoctonia solani*. *Biocontrol Sci* 19(2):99–102. <https://doi.org/10.4265/bio.19.99>
- Nishioka T, Takai Y, Mishima T, Kawaradani M, Tanimoto H, Okada K, Misawa T, Kusakari S (2016) Low-pressure plasma application for the inactivation of the seed-borne pathogen *Xanthomonas campestris*. *Biocontrol Sci* 21(1):37–43. <https://doi.org/10.4265/bio.21.37>
- Nojima H, Park R-E, Kwon J-H, Suh I, Jeon J, Ha E, On H-K, Kim H-R, Choi K, Lee K-H, Seong B-L, Jung H, Kang SJ, Namba S,

- Takiyama K (2007) Novel atmospheric pressure plasma device releasing atomic hydrogen: reduction of microbial-contaminants and OH radicals in the air. *J Phys D Appl Phys* 40(2):501–509. <https://doi.org/10.1088/0022-3727/40/2/026>
- Ochi A, Konishi H, Ando S, Sato K, Yokoyama K, Tsushima S, Yoshida S, Morikawa T, Kaneko T, Takahashi H (2017) Management of bakanae and bacterial seedling blight diseases in nurseries by irradiating rice seeds with atmospheric plasma. *Plant Pathol* 66(1):67–76. <https://doi.org/10.1111/ppa.12555>
- Oerke E-C (2006) Crop losses to pests. *J Agric Sci* 144(1):31–43. <https://doi.org/10.1017/S0021859605005708>
- Okumura T, Saito Y, Takano K, Takahashi K, Takaki K, Satta N, Fujio T (2016) Inactivation of bacteria using discharge plasma under liquid fertilizer in a hydroponic culture system. *Plasma Med* 6(3–4):247–254. <https://doi.org/10.1615/PlasmaMed.2016018683>
- Pal KK, Gardener BM (2006) Biological control of plant pathogens. *Plant Health Instruct* 2:1117–1142. <https://doi.org/10.1094/PHI-A-2006-1117-02>
- Pannong K, Lee SH, Park DH, Sim GB, Kim YH, Uhm HS, Park G, Choi EH (2014) Non-thermal plasma treatment diminishes fungal viability and up-regulates resistance genes in a plant host. *PLoS ONE* 9(6):e99300. <https://doi.org/10.1371/journal.pone.0099300>
- Park BJ, Lee DH, Park JC, Lee IS, Lee KY, Hyun SO, Chun MS, Chung KH (2003) Sterilization using a microwave-induced argon plasma system at atmospheric pressure. *Phys Plasmas* 10(11):4539–4544. <https://doi.org/10.1063/1.1613655>
- Pastor V, Luna E, Mauch-Mani B, Ton J, Flors V (2013) Primed plants do not forget. *Environ Exp Bot* 94:46–56
- Patil S, Moiseev T, Misra NN, Cullen PJ, Mosnier JP, Keener KM, Bourke P (2014) Influence of high voltage atmospheric cold plasma process parameters and role of relative humidity on inactivation of *Bacillus atrophaeus* spores inside a sealed package. *J Hosp Infect* 88(3):162–169. <https://doi.org/10.1016/j.jhin.2014.08.009>
- Pawlat J, Starek A, Sujak A, Terebun P, Kwiatkowski M, Budzeń M, Andrejko D (2018) Effects of atmospheric pressure plasma jet operating with DBD on *Lavatera thuringiaca* L. seeds' germination. *PLoS ONE* 13(4):e0194349. <https://doi.org/10.1371/journal.pone.0194349>
- Perez SM, Biondi E, Laurita R, Proto M, Sarti F, Gherardi M, Bertaccini A, Colombo V (2019) Plasma activated water as resistance inducer against bacterial leaf spot of tomato. *PLoS ONE* 14(5):e0217788. <https://doi.org/10.1371/journal.pone.0217788>
- Pérez Pizá MC, Prevosto L, Zilli C, Cejas E, Kelly H, Balestrasse K (2018) Effects of non-thermal plasmas on seed-borne diaporthe/ phomopsis complex and germination parameters of soybean seeds. *Innov Food Sci Emerg Technol* 49:82–91. <https://doi.org/10.1016/j.ifset.2018.07.009>
- Pérez-Pizá MC, Grijalba PE, Cejas E, Garcés JCC, Ferreyra M, Zilli C, Vallecorsa P, Santa-Cruz D, Yannarelli G, Prevosto L, Balestrasse K (2021) Effects of non-thermal plasma technology on *Diaporthe longicolla* cultures and mechanisms involved. *Pest Manag Sci* 77(4):2068–2077. <https://doi.org/10.1002/ps.6234>
- Pérez-Salamó I, Papdi C, Rigó G, Zsigmond L, Vilela B, Lumberras V, Nagy I, Horváth B, Domoki M, Darula Z, Medzihradsky K, Bögre L, Koncz C, Szabados L (2014) The heat shock factor A4A confers salt tolerance and is regulated by oxidative stress and the mitogen-activated protein kinases MPK3 and MPK6. *Plant Physiol* 165(1):319–334. <https://doi.org/10.1104/pp.114.237891>
- Petrov VD, Van Breusegem F (2012) Hydrogen peroxide-A central hub for information flow in plant cells. *AoB Plants* 2012:pls014. <https://doi.org/10.1093/aobpla/pls014>
- Pignata C, D'Angelo D, Fea E, Gilli G (2017) A review on microbiological decontamination of fresh produce with nonthermal plasma. *J Appl Microbiol* 122(6):1438–1455. <https://doi.org/10.1111/jam.13412>
- Pikaard CS, Scheid OM (2014) Epigenetic regulation in plants. *Cold Spring Harb Perspect Biol* 6(12):a019315. <https://doi.org/10.1101/cshperspect.a019315>
- Puač N, Gherardi M, Shiratani M (2018) Plasma agriculture: a rapidly emerging field. *Plasma Process Polym* 15(2):1700174. <https://doi.org/10.1002/ppap.201700174>
- Puligundla P, Mok C (2016) Non-thermal plasmas (NTPs) for inactivation of viruses in abiotic environment. *Res J Biotechnol* 11(6):91–96
- Puligundla P, Kim J-W, Mok C (2017) Effect of corona discharge plasma jet treatment on decontamination and sprouting of rape-seed (*Brassica napus* L.) seeds. *Food Control* 71:376–382. <https://doi.org/10.1016/j.foodcont.2016.07.021>
- Pusz KW, Kacprzyk TCR (2015) The effect of low-temperature plasma on fungus colonization of winter wheat grain and seed quality. *Pol J Environ Stud* 24(1):433–438
- Reineke K, Langer K, Hertwig C, Ehlbeck J, Schlüter O (2015) The impact of different process gas compositions on the inactivation effect of an atmospheric pressure plasma jet on *Bacillus* spores. *Innov Food Sci Emerg Technol* 30:112–118. <https://doi.org/10.1016/j.ifset.2015.03.019>
- Rossi L, Borghi M, Francini A, Lin X, Xie D-Y, Sebastiani L (2016) Salt stress induces differential regulation of the phenylpropanoid pathway in *Olea europaea* cultivars Frantoio (salt-tolerant) and Leccino (salt-sensitive). *J Plant Physiol* 204:8–15. <https://doi.org/10.1016/j.jplph.2016.07.014>
- Šamec D, Karalija E, Sola I, Vujčić Bok V, Salopek-Sondi B (2021) The role of polyphenols in abiotic stress response: the influence of molecular structure. *Plants* 10(1):118. <https://doi.org/10.3390/plants10010118>
- Selcuk M, Oksuz L, Basaran P (2008) Decontamination of grains and legumes infected with *Aspergillus* spp. and *Penicillium* spp. by cold plasma treatment. *Bioresour Technol* 99(11):5104–5109. <https://doi.org/10.1016/j.biortech.2007.09.076>
- Seol Y, Kim J, Park S, Young Chang H (2017) Atmospheric pressure pulsed plasma induces cell death in photosynthetic organs via intracellularly generated ROS. *Sci Rep* 7(1):589. <https://doi.org/10.1038/s41598-017-00480-6>
- Šerá B, Zahoranová A, Bujdáková H, Šerý M (2019) Disinfection from pine seeds contaminated with *Fusarium circinatum* Nirenberg and O'Donnell using non-thermal plasma treatment. *Rom Rep Phys* 71:701
- Sheteiwy MS, An J, Yin M, Jia X, Guan Y, He F, Hu J (2019) Cold plasma treatment and exogenous salicylic acid priming enhances salinity tolerance of *Oryza sativa* seedlings. *Protoplasma* 256(1):79–99. <https://doi.org/10.1007/s00709-018-1279-0>
- Shim D, Hwang J-U, Lee J, Lee S, Choi Y, An G, Martinoia E, Lee Y (2009) Orthologs of the class A4 heat shock transcription factor *HsfA4a* confer cadmium tolerance in wheat and rice. *Plant Cell* 21(12):4031–4043. <https://doi.org/10.1105/tpc.109.066902>
- Šimončicová J, Kaliňáková B, Kováčik D, Medvecká V, Lakatoš B, Kryštofová S, Hoppanová L, Palušková V, Hudcová D, Ďurina P, Zahoranová A (2018) Cold plasma treatment triggers anti-oxidative defense system and induces changes in hyphal surface and subcellular structures of *Aspergillus flavus*. *Appl Microbiol Biotechnol* 102(15):6647–6658. <https://doi.org/10.1007/s00253-018-9118-y>
- Simontacchi M, Galatro A, Ramos-Artuso F, Santa-María GE (2015) Plant survival in a changing environment: The role of nitric oxide in plant responses to abiotic stress. *Front Plant Sci* 6:977. <https://doi.org/10.3389/fpls.2015.00977>

- Sivachandiran L, Khacef A (2017) Enhanced seed germination and plant growth by atmospheric pressure cold air plasma: combined effect of seed and water treatment. *RSC Adv* 7(4):1822–1832
- Směkalová V, Doskočilová A, Komis G, Šamaj J (2014) Crosstalk between secondary messengers, hormones and MAPK modules during abiotic stress signalling in plants. *Biotechnol Adv* 32(1):2–11. <https://doi.org/10.1016/j.biotechadv.2013.07.009>
- Soltani A, Gholipour M, Zeinali E (2006) Seed reserve utilization and seedling growth of wheat as affected by drought and salinity. *Environ Exp Bot* 55(1):195–200. <https://doi.org/10.1016/j.envexpbot.2004.10.012>
- Sonawane SKTM, Patil S (2020) Non-thermal plasma: an advanced technology for food industry. *Food Sci Technol Int* 26(8):727–740. <https://doi.org/10.1177/1082013220929474>
- Starič P, Vogel-Mikuš K, Mozetič M, Junkar I (2020) Effects of non-thermal plasma on morphology, genetics and physiology of seeds: a review. *Plants* 9(12):1736. <https://doi.org/10.3390/plants9121736>
- Štěpánová V, Slavíček P, Kelar J, Prášíl J, Směkal M, Stupavská M, Jurmanová J, Černák M (2018) Atmospheric pressure plasma treatment of agricultural seeds of cucumber (*Cucumis sativus* L.) and pepper (*Capsicum annuum* L.) with effect on reduction of diseases and germination improvement. *Plasma Process Polym* 15(2):1700076. <https://doi.org/10.1002/ppap.201700076>
- Sthijns MMJPE, Weseler AR, Bast A, Haenen GRMM (2016) Time in redox adaptation processes: from evolution to hormesis. *Int J Mol Sci* 17(10):1649–2016
- Stoffels E, Sakiyama Y, Graves D (2008) Cold atmospheric plasma: charged species and their interactions with cells and tissues. *PIEEE Trans Plasma Sci* 36:1441–1457. <https://doi.org/10.1109/TPS.2008.2001084>
- Strange RN, Scott PR (2005) Plant disease: a threat to global food security. *Annu Rev Phytopathol* 43:83–116. <https://doi.org/10.1146/annurev.phyto.43.113004.133839>
- Sugimoto T, Watanabe K, Yoshida S, Aino M, Irie K, Matoh T, Biggs AR (2008) Select calcium compounds reduce the severity of phytophthora stem rot of soybean. *Plant Dis* 92(11):1559–1565. <https://doi.org/10.1094/PDIS-92-11-1559>
- Sundin GW, Castiblanco LF, Yuan X, Zeng Q, Yang C-H (2016) Bacterial disease management: challenges, experience, innovation and future prospects. *Mol Plant Pathol* 17(9):1506–1518. <https://doi.org/10.1111/mpp.12436>
- Suriyasak C, Hatanaka K, Tanaka H, Okumura T, Yamashita D, Attri P, Koga K, Shiratani M, Hamaoka N, Ishibashi Y (2021) Alterations of DNA methylation caused by cold plasma treatment restore delayed germination of heat-stressed rice (*Oryza sativa* L.) seeds. *ACS Agric Sci Technol* 1(1):5–10. <https://doi.org/10.1021/acsagascitech.0c00070>
- Surowsky B, Fröhling A, Gottschalk N, Schlüter O, Knorr D (2014) Impact of cold plasma on *Citrobacter freundii* in apple juice: Inactivation kinetics and mechanisms. *Int J Food Microbiol* 174:63–71. <https://doi.org/10.1016/j.ijfoodmicro.2013.12.031>
- Surowsky B, Schlüter O, Knorr D (2015) Interactions of non-thermal atmospheric pressure plasma with solid and liquid food systems: a review. *Food Eng Rev* 7(2):82–108. <https://doi.org/10.1007/s12393-014-9088-5>
- Szili EJ, Harding FJ, Hong SH, Herrmann F, Voelcker NH, Short RD (2015) The hormesis effect of plasma-elevated intracellular ROS on HaCaT cells. *J Phys Appl Phys* 48(49):495401. <https://doi.org/10.1088/0022-3727/48/49/495401>
- Tabares FL, Junkar I (2021) Cold plasma systems and their application in surface treatments for medicine. *Molecules* 26:1903. <https://doi.org/10.3390/molecules26071903>
- Tada Y, Spoel SH, Pajeroska-Mukhtar K, Mou Z, Song J, Wang C, Zuo J, Dong X (2008) Plant immunity requires conformational charges of *npr1* via s-nitrosylation and thioredoxins. *Science* 321(5891):952–956. <https://doi.org/10.1126/science.1156970>
- Takamatsu T, Uehara K, Sasaki Y, Hidekazu M, Matsumura Y, Iwasawa A, Ito N, Kohno M, Azuma T, Okino A (2015) Microbial inactivation in the liquid phase induced by multigas plasma jet. *PLoS ONE* 10(7):e0132381. <https://doi.org/10.1371/journal.pone.0132381>
- Talbi S, Romero-Puertas MC, Hernández A, Terrón L, Ferchichi A, Sandalio LM (2015) Drought tolerance in a Saharian plant *Oudneya africana*: role of antioxidant defences. *Environ Exp Bot* 111:114–126. <https://doi.org/10.1016/j.envexpbot.2014.11.004>
- Tanaka Y, Yasuda H, Kurita H, Takashima K, Mizuno A (2014) Analysis of the inactivation mechanism of bacteriophage ØX174 by atmospheric pressure discharge plasma. *IEEE Trans Ind Appl* 50(2):1397–1401. <https://doi.org/10.1109/TIA.2013.2274260>
- Tensmeyer LG, Wright PE, Fegenbush DO, Snapp SW (1981) Sterilization of glass containers by laser initiated plasmas. *PDA J Pharm Sci Technol* 35(3):93–97
- Thomas TTD, Puthur JT (2017) UV radiation priming: a means of amplifying the inherent potential for abiotic stress tolerance in crop plants. *Environ Exp Bot* 13:57–66. <https://doi.org/10.1016/j.envexpbot.2017.03.003>
- Tiwari TN, Kumar SPJ, Tiwari AK, Agarwal DK (2018) Seed coating in relation to minimizing the effects of seed ageing in rice (*Oryza sativa* L.). *J Rice Res* 10:27–32
- Toyokawa Y, Yagyu Y, Misawa T, Sakudo A (2017) A new roller conveyor system of non-thermal gas plasma as a potential control measure of plant pathogenic bacteria in primary food production. *Food Control* 72:62–72. <https://doi.org/10.1016/j.foodcont.2016.07.031>
- Trompeter F-J, Neff WJ, Franken O, Heise M, Neiger M, Liu S, Pietsch GJ, Saveljew AB (2002) Reduction of *Bacillus subtilis* and *Aspergillus niger* spores using nonthermal atmospheric gas discharges. *IEEE Trans Plasma Sci* 30(4):1416–1423. <https://doi.org/10.1109/TPS.2002.804182>
- Valifard M, Mohsenzadeh S, Kholdebarin B, Rowshan V (2014) Effects of salt stress on volatile compounds, total phenolic content and antioxidant activities of *Salvia mirzayanii*. *S Afr J Bot* 93:92–97. <https://doi.org/10.1016/j.sajb.2014.04.002>
- Vanacker H, Carver TLW, Foyer CH (1998) Pathogen-induced changes in the antioxidant status of the apoplast in barley leaves. *Plant Physiol* 117(3):1103–1114. <https://doi.org/10.1104/pp.117.3.1103>
- Varilla C, Marcone M, Annor GA (2020) Potential of cold plasma technology in ensuring the safety of foods and agricultural produce: a review. *Foods* 9(10):1435. <https://doi.org/10.3390/foods9101435>
- von Woedtke RS, Masur K, Weltmann K-D (2013) Plasmas for medicine. *Phys Rep* 530(4):291–320. <https://doi.org/10.1016/j.physrep.2013.05.005>
- Wada KC, Mizuuchi K, Koshio A, Kaneko K, Mitsui T, Takeno K (2014) Stress enhances the gene expression and enzyme activity of phenylalanine ammonia-lyase and the endogenous content of salicylic acid to induce flowering in pharbitis. *J Plant Physiol* 171(11):895–902. <https://doi.org/10.1016/j.jplph.2014.03.008>
- Wojtyła Ł, Lechowska K, Kubala S, Garnczarska M (2016) Different modes of hydrogen peroxide action during seed germination. *Front Plant Sci* 7:66. <https://doi.org/10.3389/fpls.2016.00066>
- Wu ZH, Chi LH, Bian SF, Xu KZ (2007) Effects of plasma treatment on maize seedling resistance. *J Maize Sci* 15:111–113
- Wu M-C, Liu C-T, Chiang C-Y, Lin Y-J, Lin Y-H, Chang Y-W, Wu J-S (2019) Inactivation effect of *Colletotrichum gloeosporioides* by long-lived chemical species using atmospheric-pressure corona plasma-activated water. *IEEE Trans Plasma Sci* 47(2):1100–1104. <https://doi.org/10.1109/TPS.2018.2871856>
- Xing Y, Jia W, Zhang J (2008) AtMKK1 mediates ABA-induced CAT1 expression and H<sub>2</sub>O<sub>2</sub> production via AtMPK6-coupled signalling

- in Arabidopsis. *Plant J* 54(3):440–451. <https://doi.org/10.1111/j.1365-3113.2008.03433.x>
- Xiong Q, Liu H, Lu W, Chen Q, Xu L, Wang X, Zhu Q, Zeng X, Yi P (2017) Inactivation of *Candida glabrata* by a humid DC argon discharge afterglow: Dominant contributions of short-lived aqueous active species. *J Phys D Appl Phys* 50(20):205203. <https://doi.org/10.1088/1361-6463/aa681e>
- Xu Z, Cheng C, Shen J, Lan Y, Hu S, Han W, Chu PK (2018) In vitro antimicrobial effects and mechanisms of direct current air-liquid discharge plasma on planktonic *Staphylococcus aureus* and *Escherichia coli* in liquids. *Bioelectrochemistry* 121:125–134. <https://doi.org/10.1016/j.bioelechem.2018.01.012>
- Yang W, Yin Y, Li Y, Cai T, Ni Y, Peng D, Wang Z (2014) Interactions between polyamines and ethylene during grain filling in wheat grown under water deficit conditions. *Plant Growth Regul* 72(2):189–201. <https://doi.org/10.1007/s10725-013-9851-2>
- Yang Z, Chen J, Dou R, Gao X, Mao C, Wang L (2015) Assessment of the phytotoxicity of metal oxide nanoparticles on two crop plants, maize (*Zea mays* L.) and rice (*Oryza sativa* L.). *Int J Environ Res Public* 12(12):15100–15109. <https://doi.org/10.3390/ijerp121214963>
- Yasuda H, Miura T, Kurita H, Takashima K, Mizuno A (2010) Biological evaluation of DNA damage in bacteriophages inactivated by atmospheric pressure cold plasma. *Plasma Process Polym* 7(3–4):301–308. <https://doi.org/10.1002/ppap.200900088>
- Yoshida T, Sakuma Y, Todaka D, Maruyama K, Qin F, Mizoi J, Kidokoro S, Fujita Y, Shinozaki K, Yamaguchi-Shinozaki K (2008) Functional analysis of an Arabidopsis heat-shock transcription factor HsfA3 in the transcriptional cascade downstream of the DREB2A stress-regulatory system. *Biochem Biophys Res Commun* 368(3):515–521. <https://doi.org/10.1016/j.bbrc.2008.01.134>
- Yost AD, Joshi SG (2015) Atmospheric nonthermal plasma-treated pbs inactivates *Escherichia coli* by oxidative DNA damage. *PLoS ONE* 10(10):e0139903. <https://doi.org/10.1371/journal.pone.0139903>
- Zahoranová A, Henselová M, Hudecová D, Kaliňáková B, Kováčik D, Medvecká V, Černák M (2016) Effect of cold atmospheric pressure plasma on the wheat seedlings vigour and on the inactivation of microorganisms on the seeds surface. *Plasma Chem Plasma Process* 36(2):397–414. <https://doi.org/10.1007/s11090-015-9684-z>
- Zahoranová A, Hoppanová L, Šimončicová J, Tučeková Z, Medvecká V, Hudecová D, Kaliňáková B, Kováčik D, Černák M (2018) Effect of cold atmospheric pressure plasma on maize seeds: enhancement of seedlings growth and surface microorganisms inactivation. *Plasma Chem Plasma Process* 38(5):969–988. <https://doi.org/10.1007/s11090-018-9913-3>
- Zhang S, Klessig DF (2001) MAPK cascades in plant defense signaling. *Trends Plant Sci* 6(11):520–527. [https://doi.org/10.1016/S1360-1385\(01\)02103-3](https://doi.org/10.1016/S1360-1385(01)02103-3)
- Zhang A, Jiang M, Zhang J, Ding H, Xu S, Hu X, Tan M (2007) Nitric oxide induced by hydrogen peroxide mediates abscisic acid-induced activation of the mitogen-activated protein kinase cascade involved in antioxidant defense in maize leaves. *New Phytol* 175(1):36–50. <https://doi.org/10.1111/j.1469-8137.2007.02071.x>
- Zhang X, Liu D, Zhou R, Song Y, Sun Y, Zhang Q, Niu J, Fan H, Yang S (2014) Atmospheric cold plasma jet for plant disease treatment. *Appl Phys Lett* 104(4):043702. <https://doi.org/10.1063/1.4863204>
- Zhang JJ, Jo JO, Huynh DL, Mongre RK, Ghosh M, Singh AK, Lee SB, Mok YS, Hyuk P, Jeong DK (2017) Growth-inducing effects of argon plasma on soybean sprouts via the regulation of demethylation levels of energy metabolism-related genes. *Sci Rep* 7(1):41917. <https://doi.org/10.1038/srep41917>
- Zhang Q, Zhang H, Zhang Q, Huang Q (2018) Degradation of norfloxacin in aqueous solution by atmospheric-pressure non-thermal plasma: mechanism and degradation pathways. *Chemosphere* 210:433–439. <https://doi.org/10.1016/j.chemosphere.2018.07.035>
- Zhao C, Liu B, Piao S, Wang X, Lobell DB, Huang Y, Huang M, Yao Y, Bassu S, Ciaia P, Durand J-L, Elliott J, Ewert F, Janssens IA, Li T, Lin E, Liu Q, Martre P, Müller C, Asseng S (2017) Temperature increase reduces global yields of major crops in four independent estimates. *Proc Natl Acad Sci* 114(35):9326–9331. <https://doi.org/10.1073/pnas.1701762114>
- Zhu J-K (2016) Abiotic stress signaling and responses in plants. *Cell* 167:313–324
- Zimmermann JL, Dumler K, Shimizu T, Morfill GE, Wolf A, Boxhammer V, Schlegel J, Gansbacher B, Anton M (2011) Effects of cold atmospheric plasmas on adenoviruses in solution. *J Phys D Appl Phys* 44(50):505201. <https://doi.org/10.1088/0022-3727/44/50/505201>