



Mechanisms of Plasma-Seed Treatments as a Potential Seed Processing Technology

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Plasma treatments are currently being assessed as a seed processing technology for agricultural purposes where seeds are typically subjected to pre-sowing treatments to improve the likelihood of timely and uniform germination. The aim of this review is to summarize the hypotheses and present the evidence to date of how plasma treatments affect seeds, considering that there is difficulty in standardizing the methodology in this interdisciplinary field given the plethora of variables in the experimental setup of the plasma device and handling of biological samples. The ever increasing interest for plasma agriculture drives the need for a review dedicated to seeds, which is understandable to an interdisciplinary audience of biologists and plasma physicists. Seeds are the first step of the agricultural cycle and at this stage, the plant can be given the highest probability of establishment, despite environmental conditions, to exploit the genetic potential of the seed. Furthermore, seedlings seem to be too sensitive to the oxidation of plasma and therefore, seeds seem to be the ideal target. This review intentionally does not include seed disinfection and sterilization due to already existing reviews. Instead, a summary of the mechanisms of how plasma may be affecting the seed and its germination and developmental properties will be provided and discussed.

Keywords: plasma, seeds, processing, mechanisms, germination, surface modification, stress or disease resistance

INTRODUCTION

The motivation driving plasma-seed treatment research is the importance of food. The world population is projected to increase to 10 billion by 2050 and even without increasing the food supply, it is necessary to maintain the current food production and quality [1]. Most food begins with planting seeds.

The aim of this review is to centralize the hypotheses and present the evidence to date of how plasma treatments affect seeds, considering that there is difficulty in standardizing the methodology in this interdisciplinary field given the plethora of variables in the experimental setup of the plasma device and handling of biological samples. Considering that plasma agriculture has been gaining more attention recently, it is therefore useful to have a review dedicated to seeds, which is understandable to an interdisciplinary audience of biologists and plasma physicists.

The review is organized as follows. The Seed Structure and Development section will be presented first to establish a common ground, followed by a summary of current techniques used to improve seed survival in section Seed Performance. In section Non-thermal Plasma (NTP) as a Seed Processing Technology, plasma will be introduced and the motivation for its application on seeds followed by a corroboration of recent research to provide an overview of physical, chemical, and biological mechanisms that can be triggered by plasma components is in section Mechanisms of How Non-thermal Plasma Affects Seeds and Their Subsequent Development.

SEED STRUCTURE AND DEVELOPMENT

Although very diverse, all seeds have generally evolved to contain all their needs to develop into plantlets once the environmental conditions are perceived as appropriate. The living tissues of seeds are protected by the seed coat (testa), which can vary between species and cultivars, or depend on the plants being fertile or clones unable to produce the next generation. Inside the dry mature seed, the embryo is in a partially desiccated, quiescent state, poised to germinate upon the addition of water or in other words, imbibition. It is then provided with stored foods through the endosperm during germination, a process which is the transition from an inactive to active seed that grows, ruptures the seed coat and develops from a seedling first into a plantlet, which is generally still frail and particularly sensitive to external stresses, to then a more stress-resistant autotrophic plant.

The trigger for germination requires a number of external parameters to be met, which will vary from seed to seed, but are generally a combination of water, temperature and light. Additionally, each seed has different requirements due to structural differences, particularly in the seed coat. Imbibition is the first step where the seed undergoes three stages with initially rapid, then slow and finally rapid water uptake. Water reactivates the enzymes that can repair DNA and membrane damages by using pre-existing RNA transcripts produced during seed maturation, and activates enzymes involved in beta-oxidation and amylases to break down stored oil and starch into sugars for energy and cell wall production. Proteases break down storage proteins into amino acids for protein synthesis [2].

After the third water uptake stage, the seed is swollen since the tissues have expanded and the embryo grows. The first visible sign of germination is the protrusion of the radicle, which later becomes the root. From there, the hypocotyl, which connects the root and shoot, hooks out and brings out the shoot with the cotyledon/s, then the true leaves. Once photosynthesis starts, the plantlet can grow independently from prior storages of organic matter and will only take nutrients and water from the soil and the surrounding media.

Prior to germination, there are hormones and inhibitors that prevent the process, to ensure the right environment and maximize the probability of the germinated seed to survive and thrive. The hormone abscisic acid (ABA) is known for its role in maintaining dormancy and for inhibiting germination. When this is removed by a lengthy water imbibition, another hormone

gibberellic acid (GA) is produced and germination begins. As the embryo grows, both auxin and cytokinin are involved in cell expansion and cell division, respectively, whereas later during the stressful life of the plant, hormones such as salicylic acid, jasmonic acid and ethylene will play a role in plant defense to protect it against abiotic stresses such as cold, heat, dehydration, and biotic stresses, such as herbivores, viral, fungal and bacterial pathogens. More information about plant defense can be found in Andersen et al. [3].

SEED PERFORMANCE

The best chance for survival is to provide the seed with an opportunity to germinate from the very beginning, assuming they are not dead, and for food production, there are additional criteria beyond successful germination which are germination uniformity and rate for a single harvest when done on an industrial scale. For this reason, many centuries ago, a method called priming was developed to ensure a more uniform and faster germination.

Seed priming is a method which can increase plant growth parameters, such as germination rate and uniformity and contribute to higher yields and greater plant resistance. As reviewed by Pawar and Laware [4] and Lutts et al. [5], the concept of priming is to provide water and activate the metabolism of the seed to repair damage before continuing the embryo development and the emergence of the root.

Priming is frequently applied using water (hydro-priming), which requires soaking the seeds for a given timeframe. This water treatment can be modified to ameliorate germination rate, efficiency and uniformity with the addition of salts (halo-priming), solutes to change the osmotic pressure (osmo-priming), micronutrients like boron and iron (nutri-priming), hormones like gibberellic acid (hormonal priming) or beneficial microorganisms, such as *Pseudomonas* species (bio-priming), and metallic nanoparticles like iron and silver (nano-priming). Priming can also be done without water by using a solid and non-soluble material such as sand or clay called matrix priming [4].

Depending on the seed and its structure, it can be primed with wet treatments by soaking in cold, warm, boiling water or dry treatments using dry heat or microwaves. Seeds can also be primed using acid scarification and physical scarification. Seeds, specifically their seed coats, can also be modified with compounds such as selenium or salicylic acid [6] or agents that are protectants, nutrients, symbionts, soil adjuvants (hydrogels) and colorants [7]. Protectants, such as pesticides, and colorants make up the bulk of coatings and are applied mostly to crops and vegetables to mainly deter insects (44%), weeds, and fungi [8].

Pesticides in the seed coatings can transfer into the soil through rain and enter the groundwater and wastewater treatment plants. Since these compounds are highly toxic, persist for a long time and become more toxic with time when held in storage, remediation methods, used to remove toxic chemical compounds, can be done with microorganisms, clay, polymeric

materials or UV- H_2O_2 and UV- ozone, and hydroxyl radicals and at times, even require additional water resources [9].

Although protective coatings are important and occupy a multi-billion-dollar market, the amount of investment in remediation techniques highlights that it would be beneficial to consider alternatives to minimize pesticide use. For this reason, alternatives have been considered such as biocontrol using fungi or bacteria, biopesticides derived from natural compounds such as grapefruit seed extract [10], physical methods such as ultrasound [11, 12] as well as genetic engineering [13]. It would also be ideal to find a method with minimal energy consumption in view of energy savings considering that energy input is five to ten times greater than the output in the form of food in North America [14].

NON-THERMAL PLASMA (NTP) AS A SEED PROCESSING TECHNOLOGY

Ideally, more effective solutions for seed treatment to ensure rapid and uniform germination should not include toxic residues, consume little energy, have low penetration depth to avoid injuring cells, and favor long storage time [15], while subsequently supporting optimal seed development. These criteria can possibly be met with non-thermal plasma (NTP) treatments.

Plasma is an ionized gas that can be ignited under low or atmosphere pressure conditions. The plasma composition depends on the operating parameters such as voltage, frequency, humidity, flow rate, and gas mixture. Gases such as argon, oxygen, nitrogen, helium, and/or air can be ionized by electric fields to form electrons, ions, UV, thermal radiation and reactive species. Specifically, air plasmas contain reactive oxygen species (ROS) such as superoxide (O_2^-), hydrogen peroxide (H_2O_2), hydroxyl radical (OH^\cdot), singlet oxygen (1O_2), and ozone (O_3) and reactive nitrogen species (RNS) such as nitric oxide (NO^\cdot), peroxy nitrite and nitrogen dioxide radical (NO_2^\cdot) [16]. Han et al. [17] and Laroussi [18] describe the types of plasma treatments in detail. Šimončicová et al. [19] describe the types of plasma treatments for biological applications. In short, they include dielectric barrier discharge (DBD) as the most common plasma source, followed by plasma jet, corona, microwave, radiofrequency, and gliding arc. The DBD generates plasma by alternating high voltage (kV) between two electrodes, one or both of which are insulated by a dielectric to prevent electric arcs. The DBD may generate the plasma in a volume of gas between the electrodes (VDBD) or on the surface of a dielectric adjacent to electrodes (SDBD). In a plasma jet, there is usually a DBD excitation of gas flowing in a thin tube. Corona ignites plasma at the tip of a sharp edge and forms diffuse plasma toward the ground electrode. Microwave plasma is produced using a magnetron at a very high frequency in the GHz range, whereas radiofrequency plasma is ignited in the MHz range; both are ignited in a vacuum chamber at low gas pressure. Gliding arc generates an arc at the shortest distance between two diverging electrodes, which then expands. The seeds and seedlings can be treated directly with the plasma or indirectly at a distance away

from the plasma. They can also be soaked or watered using liquids exposed to plasma. These liquids are considered as plasma-activated media (PAM) and if water is used, it is called plasma-activated water (PAW). Comparing the gaseous and aqueous treatments, similar effects on macroscopic plant properties have been reported [20, 21].

Plasma treatment may enhance seed survival without toxic residues since all the constituents in plasmas may be found in nature and recombine shortly afterwards. Moreover, components in plasma have approximately 10 nm deep penetration, limiting it to surface functionalization [12]. Importantly, plasma treatments are considered to be low maintenance with low energy costs [22]. Therefore, many studies have been performed involving plasma treatments of agronomic interest, such as quinoa, basil, tomato, wheat, radish, soybean, mung bean, rice, Ajwain and Umbu and seeds deemed important for the landscape like Norway spruce [23].

Randeniya and de Groot [22] and Puac et al. [24] reviewed the observed effects on germination and subsequent plant growth. The extensive list of these effects in this review has been summarized in **Figure 1**. It can increase germination probability and biomass [25] or increase disease resistance or stress resistance [26, 27]. Additionally, it can accelerate or delay germination and subsequent development [28], decrease water consumption [29], decrease levels of microbial pathogens or insects [30, 31], without detectable toxic residues [20]. Molina et al. [32] proposed to make a hydro-absorbant polymer coating with short plasma treatments on specific seed types, and Kopacki et al. [33] suggested to use plasma for seed coatings against fungal pathogens.

Other than treating the seed or plant directly, plasma treatment can also be used on the plant's surroundings by degrading volatile organic compounds in the soil to improve soil health [34, 35]. It may also have potential as an alternative to fungicide [36] and be implemented in industry as field studies have shown [16, 37].

Table 1 shows the legend describing the categories of **Table 2**, which is a compilation of papers described in four categories: seed coat modification, growth parameters, metabolism, and disease or stress resistance and further divided by the scale of information i.e., macroscopic, microscopic or molecular properties. Seed disinfection and sterilization were intentionally left aside and can instead be found in more detail in the food processing field [108].

MECHANISMS OF HOW NON-THERMAL PLASMA AFFECTS SEEDS AND THEIR SUBSEQUENT DEVELOPMENT

Quite consistently, most reports refer to optimized plasma setups that can significantly change germination and plant growth parameters. For example, germination rate may be accelerated, shoot and root lengths may be longer [68] and more branching of the roots [25] or stronger root system [85] were reported although it is difficult to know the causative agent behind these effects due to varying plasma-seed treatment methodologies.

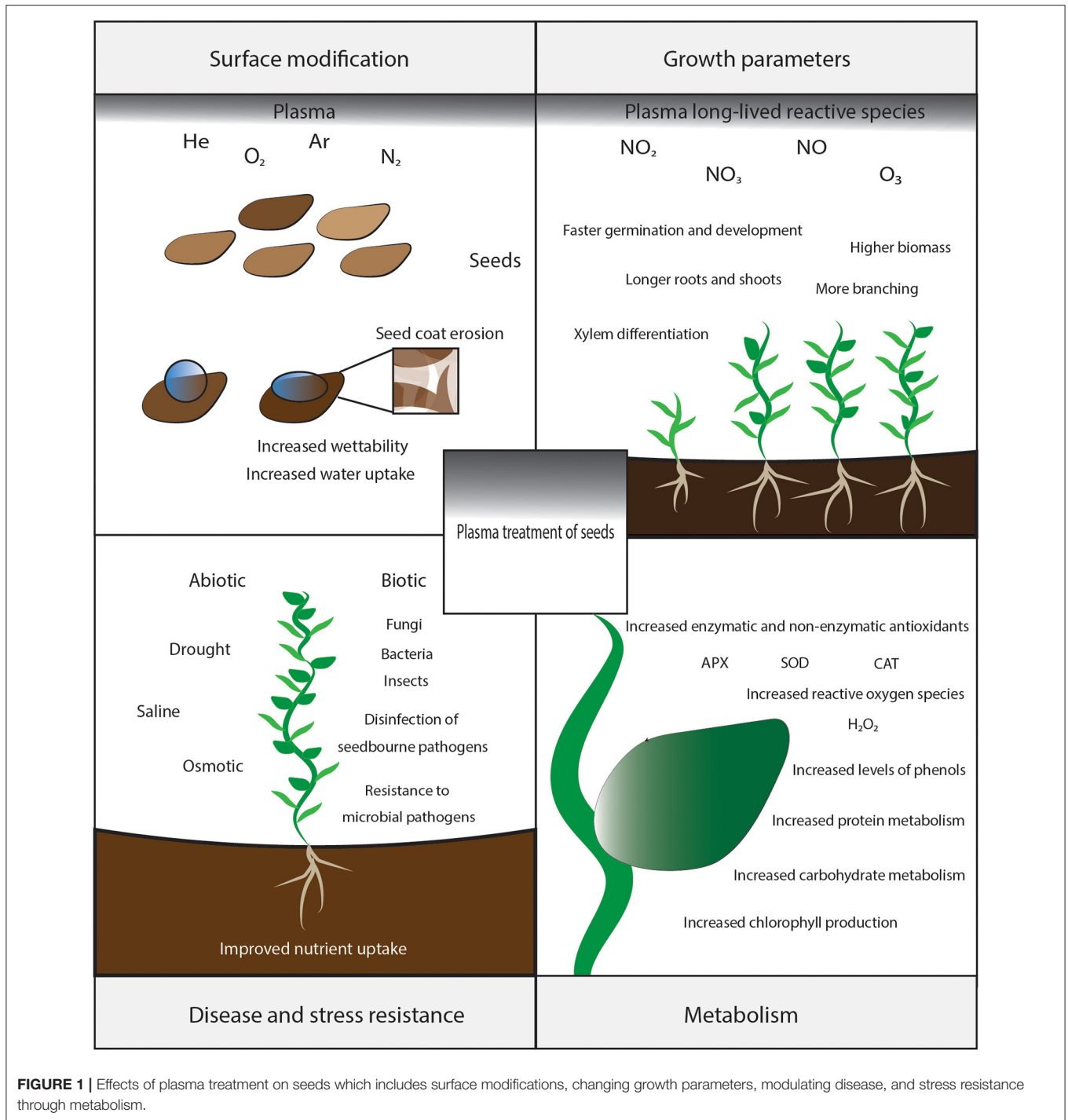


FIGURE 1 | Effects of plasma treatment on seeds which includes surface modifications, changing growth parameters, modulating disease, and stress resistance through metabolism.

Not all observe the same effects and instead, plant growth can be improved without changing germination rate [49] or scientists have strong variation in their experiments [53, 69]. This could mean that further optimization is required, which is time-consuming considering the number of variables in the experimental design. It is not yet clear by which mechanism(s) these effects arise but understanding this will simplify the

experimental design and potential scale up for the future so that the results are reproducible. Here, we take a closer look at the physical, chemical, and biochemical factors derived from plasma treatments to have a more detailed understanding of what is happening to the seed. A summary of the plasma-seed interactions at the seed surface and at a molecular level are given in **Figures 2, 3**, respectively.

TABLE 1 | Legend describing each category of **Table 2** for the type of plasma and seed used in the study as well as the main findings (see this table for a description of the categories).

Category	Description
Plasma	
Geometry	Volume or surface dielectric barrier discharge (VDBD/SDBD), radiofrequency (RF), jet
Pressure	Atmospheric or low
Gas type	Oxygen, nitrogen, argon as single or admixtures
Seed type	
Radish, wheat, rice etc.	
Micro(organism)	
Bacteria or fungi or insect	Native or artificial contamination of a microorganism or organism (pest)
Main findings	
Seed coat modification	Wettability, water uptake, morphology, surface chemistry
Growth parameters	Germination rate, root length, shoot length, seed vigor
Metabolism	Antioxidant enzymes, proline, soluble sugars
Disease or stress resistance	Plants grown in stressful conditions or include molecular component which contributes toward resistance
Scale	
Macroscopic	Seen by eye
Microscopic	Seen using a microscope (mostly light or scanning electron)
Molecular	Enzymes, proteins, DNA, RNA, DNA modification

Physical Factors

The physical factors such as heat, ultraviolet, and electromagnetic fields and mechanical scarification are the first contact point with the seed coat and may then trigger downstream consequences from this initial interaction. In the following section, each physical factor and its effect will be presented individually.

Heat

The temperature of plasma treatments can range from room temperature up to 90°C, so in principle it is possible to have an effect depending on the temperature and treatment time although not many authors think that increased temperature is responsible for the changes in plants. Temperature is monitored in a few studies by measuring the electrode temperature, calculating the gas temperature from spectra or measuring the temperature of the seed directly using an infrared camera or thermocouple [47, 109] but it has not yet been done on a molecular level by assessing the seed or plant response. Kitazaki et al. [110] compared plasma and heat treatments by heating the seeds on a hot plate but did not see the same effect on the plant development.

Others have tried to look into heat shock proteins (HSPs), which are induced with temperatures ranging from 31 to 37°C, but HSPs are often not exclusively induced by heat. They may also accumulate under oxidative stress, high intensity irradiation, and desiccation [111]. Iranbakhsh et al. [78] treated wheat seedlings with plasma and observed increased expression in heat shock factor A4A in both the root and shoot system in correlation with

an increase of growth parameters and mitigating the negative effect of salinity stress. They only reached a maximum of 29°C in a 2 min plasma treatment, suggesting that heat alone is not responsible for the observed effects in this particular study but the role of HSPs during plasma treatment remains unclear since it was shown not to change in the study by Mildažiene et al. [53].

Ultraviolet Light (UV)

The role of high-energy photons in plasma-seed treatments has been controversial since UV has had a negligible effect so far but the effects of UV on seeds and plants could theoretically contribute to the wettability or growth enhancement effects indirectly; for example, by producing radicals or reactive oxygen species (ROS) such as ozone [60]. Gao et al. [52] checked the effects of UV separately from plasma and observed that UV had only a minor contribution toward the seed wettability. Sarinont et al. [102] also reported that there was no effect from UV when they saw the lack of growth enhancement effect after they blocked UV with a quartz plate.

It is known that just UV-B can accelerate germination of safflower seeds but then negatively affects growth [112]. Noble [113] made the same conclusions with kale, cabbage, radish and agave seeds. Likewise, Sadeghianfar et al. [114] showed accelerated germination of maize and sugar with UV-C treatment but instead, saw an increase in plant growth parameters and suspected this may be due to breaking down the seed coat and increase in temperature.

There may be differences in effects depending on the wavelength since it has been shown that UV-A had a more pronounced effect than UV-C but both were able to accelerate the germination rate and improve growth parameters [115]. On the one hand, UV is often associated with inducing DNA damage. Prakrajang et al. [46] compared gamma radiation with plasma and saw only with gamma irradiation that the plants did not grow well and thus suspected it was induced DNA damage. On the other hand, plants treated with UV were able to better cope with drought stress, possibly by activating DNA repair mechanisms [116]. This may be due to an increase in phenolic compounds, which often have a role in disease or stress resistance and this response can be triggered by intense UV light which is accompanied by high temperature and photo-oxidative damage in nature [117].

Babajani et al. [59] and Iranbakhsh et al. [118] both considered that plasma-derived UV may be detected by photoreceptors which then might affect secondary metabolism and trigger stress responses if the treatment is done briefly. UV is also linked with photomorphogenesis and cell elongation, division, and differentiation [119]. Iqbal et al. [63] compared laser and plasma treatment separately on seeds and saw similar types of effects: damage to the seed coat, an increase in water uptake and protein content.

Electromagnetic Fields (EMF)

Pauzaitė et al. [23] and Mildažiene et al. [53] also attributed the changes in growth parameters to radiation since Mildažiene et al. [53] saw similar protein expression profiles when comparing seeds treated with plasma or electromagnetic fields (EMF). This is

TABLE 2 | Collection of plasma-seed treatment papers.

Citation	Plasma	Seed type	Micro (organism)	Main findings	Scale
Iranbakhsh et al. [38]	DBD; atm pressure; Ar	Hemp		Growth parameters, metabolism	Macroscopic and molecular
Kang et al. [39]	1) Arc discharge; low or atm pressure; underwater 2) DBD; low and atm pressure; (0.6–1 atm); not clear	Rice	<i>Fusarium fujikuroi</i>	Seed coat modification, growth parameters, disinfection/disease resistance	Macroscopic
Billah et al. [40]	DBD; low pressure (400 torr); air	Black gram		Seed coat modification, growth parameters, metabolism	Macroscopic and molecular
Rezaei et al. [41]	Not clear; atm pressure; air	Hyssop		Tissue modification (dried leaves)	Macroscopic
Koga et al. [42]	DBD; atm pressure; humid air	Radish		Seed coat modification (color)	Macroscopic
Ghasempour et al. [43]	DBD; atm pressure; Ar	Catharanthus roseus		Growth parameters, metabolism	Macroscopic and molecular
Mujahid et al. [44]	DBD; atm pressure; He and O ₂	Grape cultivar Muscat of Alexandria		Growth parameters, metabolism	Macroscopic and molecular
Filatova et al. [45]	CCP RF; low pressure (200 Pa); air	Maize, wheat, lupine	Native fungi, <i>Fusarium culmorum</i>	Growth parameters, metabolism, disinfection/disease resistance	Macroscopic and molecular
Prakrajang et al. [46]	Not given; not given; Ar	Chili pepper		Growth parameters	Macroscopic
Kobayashi et al. [47]	DBD; atm pressure; air	Arabidopsis (seedlings)		Growth parameters	Macroscopic
Dawood [48]	RF; low pressure; Ar	Moringa		Seed coat modification, growth parameters	Macroscopic and microscopic
Sidk et al. [49]	Plasma jet/plume; atm pressure; He	Corn and eggplant		Growth parameters	Macroscopic
Ambrico et al. [50]	DBD; atm pressure; air	Basil		Seed coat modification, growth parameters,	Macroscopic and microscopic
Seddighinia et al. [51]	DBD; atm pressure; Ar	Bitter melon		Growth parameters	Macroscopic, microscopic
Gao et al. [52]	DBD; atm pressure; air	Pea		Seed coat modification, growth parameters	Macroscopic, microscopic
Mildažiene et al. [53]	CCP RF; low pressure (200 Pa); air	Sunflower		Growth parameters, metabolism	Macroscopic and molecular
Šerá et al. [54]	DBD; atm pressure; air	Pine		Growth parameters, disinfection	Macroscopic
Cui et al. [55]	DBD; atm pressure; air	Arabidopsis		Growth parameters, metabolism	Macroscopic and molecular
Liu et al. [56]	DBD jet; atm pressure; N ₂ , O ₂ , air	Radish, mung bean, wheat, tomato, lettuce, mustard, Dianthus and sticky bean		Growth parameters	Macroscopic
Los et al. [57]	DBD; atm pressure; air	Wheat		Seed coat modification, growth parameters, metabolism	Macroscopic and molecular
Moghanloo et al. [58]	DBD; atm pressure; Ar	Astragalus frida		Growth parameters, metabolism	Macroscopic and molecular
Pérez-Pizá et al. [36]	Needle to plane DBD; atm pressure; N ₂ , O ₂	Soybean		Seed coat modification, growth parameters, metabolism	Macroscopic and molecular
Babajani et al. [59]	DBD; atm pressure; Ar	Melissa officinalis		Growth parameters, metabolism	Macroscopic and molecular
Lotfy et al. [60]	Plasma jet; atm pressure; N ₂	Wheat		Seed coat modification (water uptake), growth parameters	Macroscopic
Bafoil et al. [61]	DBD; atm pressure; air	Arabidopsis		Seed coat modification, growth parameters	Macroscopic, microscopic?, and molecular
Singh et al. [62]	RF; low pressure; (0.40 mbar) O ₂ and Ar	Basil		Growth parameters, metabolism	Macroscopic and molecular
Iqbal et al. [63]	Not clear; low pressure; Ar	Wheat		Seed coat modification, growth parameters, disease resistance	Macroscopic and molecular

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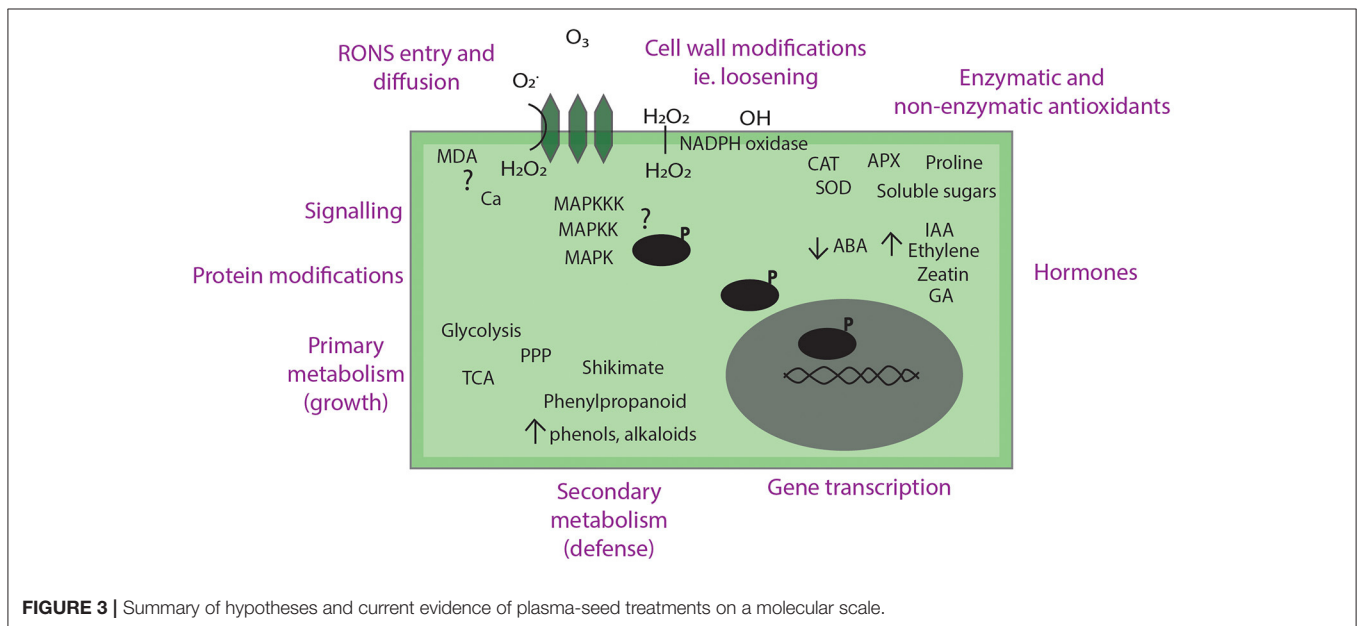
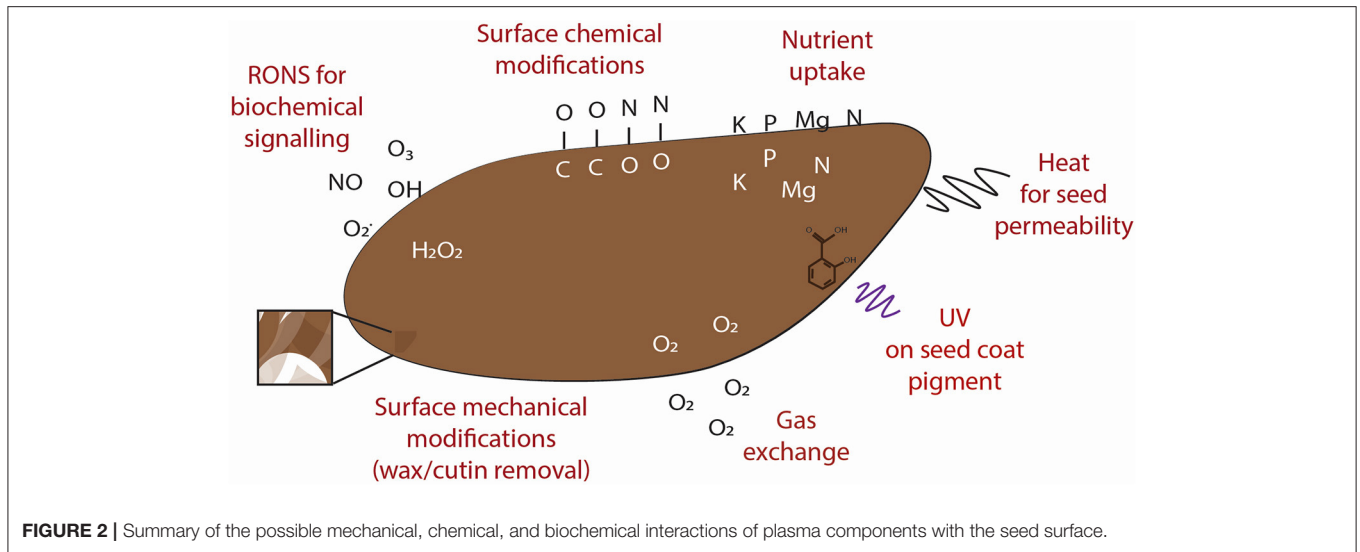
TABLE 2 | Continued

Citation	Plasma	Seed type	Microbe	Main findings	Scale
Islam et al. [64]	DBD; low pressure (10 Torr); air, Ar, O ₂	Rapeseed, mustard		Growth parameters, metabolism	Macroscopic and molecular
Kabir et al. [65]	DBD; low pressure (10 Torr); air, Ar, O ₂	Wheat		Seed coat modification, growth parameters, metabolism	Macroscopic and molecular
Afsheen et al. [66]	RF capacitive; low pressure; Ar	Wheat	Beetle	Seed coat modification, pest resistance	Macroscopic
Lo Porto et al. [67]	RF; low pressure (800 mTorr); N ₂ , O ₂	Asparagus		Seed coat modification, growth parameters	Macroscopic
Jiang et al. [68]	ICCP RF; low pressure (150 Pa); He	Tomato		Growth parameters	Macroscopic
Hosseini et al. [69]	CCP RF; low pressure; N ₂	Artichoke		Seed coat modification, growth parameters, metabolism	Macroscopic, microscopic and molecular
Tounekti et al. [70]	DBD; atm pressure; He	Coffee and grape seeds		Growth parameters	Macroscopic
Zhang B. et al. [37]	CCP glow RF; low pressure (30-200 Pa); air, He	Maize, peppers, wheat, soybeans, tomatoes, eggplants, pumpkins		Growth parameters, metabolism	Macroscopic and molecular
Khatami and Ahmadinia [71]	Gliding arc; atm pressure; air	Pea, Zucchini	Native microflora	Growth parameters	Macroscopic
Pawlat et al. [72]	DBD plasma jet; atm pressure; He and N ₂	Thuringian Mallow		Seed coat modification, growth parameters	Macroscopic and microscopic
Rahman et al. [73]	DBD; low pressure (10 Torr); air, Ar, O ₂	Wheat		Seed coat modification, growth parameters, metabolism	Macroscopic, microscopic and molecular
Pawlat et al. [72]	Gliding arc; atm pressure; N ₂	Thuringian Mallow		Seed coat modification, growth parameters	Macroscopic and microscopic
Hayashi et al. [74]	RF; low pressure (20-80 Pa); O ₂ , Ar	Arabidopsis, radish		Growth parameters, metabolism	Macroscopic and molecular
Matra [75]	Plasma flashlight; atm pressure Ar, O ₂	Sunflower		Growth parameters	Macroscopic
Bafoil et al. [76]	1) DBD; atm pressure; air 2) plasma jet; atm pressure; He	Arabidopsis		Seed coat modification, growth parameters	Macroscopic, microscopic
Măgureanu et al. [25]	DBD (fluidized); atm pressure; air	Tomato		Growth parameters	Macroscopic
Štěpánová et al. [77]	DBD; atm pressure; air	Cucumber and pepper		Seed coat modification, growth parameters	Macroscopic and microscopic
Iranbakhsh et al. [78]	DBD; atm pressure; Ar	Wheat		Growth parameters, metabolism, stress resistance	Macroscopic and molecular
Iranbakhsh et al. [79]	DBD; atm pressure; Ar	Chili pepper		Growth parameters, metabolism	Macroscopic, microscopic and molecular
Pauzaitė et al. [23]	CCP RF; low pressure (60 Pa); air	Norway spruce		Growth parameters	Macroscopic and molecular
Park et al. [80]	DBD; atm pressure; N ₂ and air	Barley		Seed coat modification, growth parameters, metabolism	Macroscopic and molecular
Zhang J. et al. [81]	DBD; atm pressure; Ar	Soybean		Growth parameters	Macroscopic
Shapira et al. [82]	RF inductive; low pressure; air	Pepper and lentil		Seed coat modification	Microscopic
Lotfy (36b)	Plasma jet; atm pressure; N ₂	Watermelon		Seed coat modification, growth parameters	Macroscopic
Wang et al. [83]	DBD; atm pressure; air, N ₂	Cotton		Seed coat modification	Microscopic
Kim et al. [84]	Corona discharge plasma jet; atm pressure; air	Broccoli	Native Aerobic bacteria, molds and yeasts, <i>B. cereus</i> , <i>E. coli</i> , <i>Salmonella</i> spp.	Growth parameters, metabolism	Macroscopic and molecular

(Continued)

TABLE 2 | Continued

Citation	Plasma	Seed type	Microbe	Main findings	Scale
Mildažiene et al. [85]	CCP RF; low pressure (60 Pa); air	Purple coneflower		Growth parameters	Macroscopic and molecular
Li et al. [86]	DBD; atm pressure; air	Wheat		Seed coat modification, growth parameters, metabolism	Macroscopic, microscopic, molecular
Sera et al. [87]	1) gliding arc; atm pressure; humid air 2) microwave plasma discharge; low pressure (140 Pa); Ar, O ₂	3 cultivars of hemp		Growth parameters	Macroscopic
Puligundla et al. [88]	Corona discharge plasma jet; atm pressure; air	Rapeseed	Native	Growth parameters, metabolism	Macroscopic and molecular
Puligundla et al. [89]	Corona discharge plasma jet; atm pressure air	Radish	Native	Growth parameters, metabolism	Macroscopic and molecular
Gómez-Ramírez et al. [90]	1) DBD; low pressure (500 mbar); dry air 2) RF; low pressure (0.1 mbar); dry air	Quinoa		Seed coat modification, growth parameters	Macroscopic, microscopic
Guo et al. [91]	DBD; atm pressure; air	Wheat		Seed coat modification, growth parameters, metabolism, stress resistance	Macroscopic, microscopic, molecular
Zhang et al. [92]	Needle to plane DBD; atm pressure; Ar	Soybean		Growth parameters, metabolism	Macroscopic, molecular
da Silva et al. [93]	DBD; atm pressure; air	Mimosa		Seed coat modification, growth parameters	Macroscopic and microscopic
Meng et al. [94]	DBD; atm pressure; air, Ar, O ₂ , N ₂	Wheat		Seed coat modification, growth parameters, metabolism	Macroscopic, microscopic, molecular
Nalwa et al. [95]	Glow discharge; low pressure (0.2 mbar); O ₂	Bell pepper		Seed coat modification, growth parameters,	Macroscopic, microscopic
Junior et al. [96]	Plasma jet DBD; atm pressure; He	Mulungu		Seed coat modification, growth parameters	Macroscopic, microscopic
Zahoranová et al. [97]	DBD; atm pressure; air	Wheat	Native	Seed coat modification, growth parameters	Macroscopic
Zhou et al. [98]	Plasma jet array; atm pressure; He, N ₂ , air, O ₂	Mung bean		Seed coat modification, growth parameters, metabolism	Macroscopic, microscopic, molecular
Khamsen et al. [99]	Hybrid microcorona discharge; atm pressure; air, Ar;	Rice	Native fungi	Seed coat modification, growth parameters	Macroscopic and microscopic
Li et al. [16]	CCP RF; low pressure (150 Pa); He	Peanut		Seed coat modification, growth parameters	Macroscopic
Gholami et al. [100]	CCP RF; low pressure; air	Ajwain		Seed coat modification, growth parameters	Macroscopic
Matra [101]	Plasma flashlight; atm pressure; Ar	Radish		Growth parameters	Macroscopic
Sarinont et al. [102]	DBD; atm pressure; air, O ₂ , NO, He, Ar, N ₂	Radish		Growth parameters	Macroscopic
Dobrin et al. [103]	DBD; atm pressure; air	Wheat		Seed coat modification, growth parameters	Macroscopic
Stolárik et al. [104]	DBD; atm pressure; air	Pea		Seed coat modification, growth parameters, metabolism	Macroscopic, microscopic, molecular
Munkhuu et al. [105]	Not clear; not clear; not clear	Clover		Growth parameters	Macroscopic
Ji et al. [106]	1) DBD; atm pressure; Ar, N ₂ , air 2) microwave plasma torch for NO; N ₂ , O ₂	Coriander		Seed coat modification, growth parameters	Macroscopic
Kadowaki and Kurisaka [107]	DBD; atm pressure; air	Arabidopsis		Growth parameters	Macroscopic



not entirely surprising since pulsed electric fields also affect seed germination [120, 121]. It needs to be kept in mind though that electric field treatment is also accompanied by oxidative stress and ozone [122] where ozone has been suggested by Patwardhan and Gandhare [123] to be the main effective parameter in the treatment.

Static or alternating magnetic fields can also change germination probability, growth rates, increase root, and shoot length, change redox status of plants possibly by increasing hydrogen peroxide (H_2O_2), altering photosynthesis, alleviating drought stress or increasing mineral content [124, 125]. Arguably, UV may have a role but a minor contribution in terms of direct effect considering that the above studies used several hours long UV treatments to have an effect whereas most plasma treatment are in the seconds or minutes range. Nevertheless, photons and electromagnetic fields can

still possibly contribute indirectly through the production of RONS.

Mechanical Scarification and Erosion

In terms of mechanical effects, it has been suggested that altering the seed coat may play a role in modifying germination rate. Typically, a seed has four layers: the cuticle, epidermis, hypodermis, and parenchyma. The differences in the microstructures and chemistry of these layers determine differences between species and even cultivars. The seed coat role is like a water modulator; it controls the entry of water so it can be absorbed slowly by the cotyledons to minimize or avoid imbibition damage [126].

It has been suggested that the removal of the lipid layer allows for better access to water, a requirement for triggering germination [127]. Bafoil et al. [61] showed the importance

of the seed coat by using mutants of *Arabidopsis* plant model *Ler* and *Col-0* ecotypes and showed the rearrangement of lipid components, changes in lignin and seed coat erosion. Many, although not all authors have observed with scanning electron microscopy (SEM) that seed surfaces treated with plasma have an eroded appearance [52, 83, 86, 93, 96, 104], where Mildažiene et al. [128] only saw etching on the seed surface facing plasma treatment and others did not see any changes [29, 110, 129].

A majority of these authors have been able to correlate these changes with increased water uptake. For example, Pawlat et al. [72] observed that plasma treatment changed the seed structure by removing the upper cuticle layers covered with wax, a polymer present to prevent water loss under heat stress, and may form micro-pores to aid water absorption. Bafoil et al. [61] also worked with an *Arabidopsis* mutant *gtap5*, which is not able to make suberin or cutin and saw that plasma was not able to improve the germination without these polymers in the seed coat, suggesting their importance. This waxy layer was even considered as a parameter in the experimental design of a study done by Park et al. [80]. They used two seed types, one with and the other without a waxy layer, and their results indirectly implied that this waxy layer plays a role in the effect that plasma treatment will have on the seeds, suggesting plasma indeed may be improving the seed coat permeability, considering wax limits water loss and controls gas exchange.

Billah et al. [40] pointed out that there may be exothermic reactions from the plasma that release heat and may melt the wax due to its low evaporation temperature of 37°C or eroded by reactive species. This was also pointed out by Holc et al. [130]. Wang et al. [83] also suggested that through surface modification via etching, the seed is able to absorb water through increased hydrophilicity. This enhanced water absorption by modifying the seed structure is further supported by others who observed the degradation of cellulose on seed surfaces [131]. Currently, the analysis of components with FTIR-ATR is limited to cellulose since it is difficult to differentiate between different organic plant components like cellulose, hemicellulose, pectins, etc. Wang et al. [83] used both FTIR-ATR to measure seed surface changes as well as FTIR to analyze the gas exhaust from the plasma treatment. They needed to omit wavenumbers i.e., peaks below 1,500 cm^{-1} that were difficult to assign to specific functional groups during analysis but also suggested that the spectral bands are mainly attributed to cellulose rather than wax.

Junior et al. [96] showed that water may be guided differently after plasma treatment due to surface modifications. They observed that the hilum increased the amount of water absorption, the micropyle had a more open configuration and in particular, the water absorption was improved mainly through the hilum rather than micropyle. In any case, by thinning the seed coat, it is logical to assume that water will be more readily absorbed.

Interestingly, the water absorption can be controlled by the plasma treatment using different gases and coating thickness as mentioned by Volin et al. [28]. Depending on the working gas, 0.5–2 μm thick coatings were applied and their thickness modified imbibition.

This suggests that the seed coat thickness can be mechanically modified by etching or by changing the chemical properties.

Despite adding to the thickness with an additional layer of coating, germination was improved in a few instances, which highlights the importance of chemistry, but it is difficult to separate the etching effect from the chemistry in this study. As it still remains, it is not known yet whether this increased permeability is principally due to mechanical mechanisms such as etching as Pawlat et al. [132] suggested, a combination of both mechanical and chemical as mentioned by Gómez-Ramírez et al. [90], Tounekti et al. [70], and Park et al. [80] or solely due to chemistry.

SEM is an insightful tool, which can provide quick qualitative results of the plasma-seed treatment. Nevertheless, caution should be exercised when interpreting SEM images because plant genetics influence the seed coat pattern. Otherwise, observed changes might already be pre-existing and should instead be attributed to biological variation rather than plasma treatment and therefore, using the same seed before and after treatment is recommended.

Pawlat et al. [132] noticed that the seed shape influences the type of change affecting the seed and showed in their SEM images that the seed edge was torn off whereas the middle grew in sharpness. This brings attention to the fact that this process needs to be delicately handled. For example, Cui et al. [55] used tape to prevent the movement of seeds during the plasma treatment but this may affect the seed coat especially if it is done in the presence of moisture. As a result, it seems that there is a limit to how much information can be extracted from surface analysis using microscopy. Instead, it would be useful to further explore the chemical modifications since this is currently limited at the moment in the literature.

It may very well be that the chemistry is sufficient to affect downstream processes considering that an effect in growth parameters without visible seed coat modifications has been observed [57]. Mildažiene et al. [85] also observed positive growth effects using vacuum and EMF without visibly changing the seed coat structure using SEM. It may also be the case that the results will depend partly on whether there is physical or physiological dormancy meaning whether dormancy is due to the seed coat or embryo.

Chemical Factors

On the one hand, etching may play more of a role in certain seed types with impermeable seed coats but, on the other hand, it may be that a specific concentration and/or mixture of reactive species from a higher power plasma is required to observe an effect. In the latter, mechanical damage might merely be a side effect, which too can contribute to enhanced water absorption but is not the primary factor. For this reason, chemical factors will now be discussed in the next section.

Nutrient Absorption

In addition to analyzing mechanical damage, SEM can be coupled with energy dispersive X-rays (EDX) to look at the composition of seed surface. Other methods such as X-ray Photoelectron

Spectroscopy (XPS) and micro X-ray fluorescence spectroscopy (μ -XRF) can also be used to acquire information about the elemental distribution. It has been observed by several authors like Pérez-Pizá et al. [36] and da Silva et al. [93] that lipid layers undergo chemical oxidation, which can therefore improve interaction with water.

Shapira et al. [82] found that irreversible wettability is not due to electric charging, which could indirectly imply that it may be done chemically. Pérez-Pizá et al. [36] also correlated the increased hydrophilicity with oxidized seed using nitrogen and oxygen plasmas. This perhaps suggests that hydrophilicity again is done through chemical rather than mechanical changes. This may not be entirely dependent on the gas type but rather about producing an appropriate profile of reactive species at sufficient concentrations that will oxidize the outermost lipids. It has been shown by Gómez-Ramírez et al. [90] using XPS and EDX that plasma treatment can oxygenate carbon and deposit nitrogen groups on the seed surface. They hypothesized that these elements, as well potassium, are later absorbed by the seed in the presence of water [133].

Ambrico et al. [50] instead used μ -XRF and showed the concentration and redistribution of macro- and micronutrients such as potassium after plasma treatment. As an example, on the one hand, the diffusion of potassium into the seed interior may improve the germination through enzyme activation, help with water retention, or detoxify ROS [134]. On the other hand, potassium at the surface can be interpreted as seed damage since it may be used as an indicator of cell membrane integrity [135]. Interestingly, Zhou et al. [98] exposed seeds to plasma-treated water and they had the lowest leakage rate by measuring electrical conductivities, which is used to measure the cell membrane integrity. This mobilization of nutrients perhaps is not lost to the environment but is loosened and absorbed immediately by the seed [136].

Gas Exchange

When considering gases, it could be that oxygen on the surface is responsible for not only increased wettability but may also assist in seed respiration. Considering that oxygen is another requirement for germination, Sarinont et al. [102] observed oxygen, NO and nitrogen gas to be the most effective for plant growth but fumigation with oxygen gas already had an effect on growth parameters, albeit mild compared to plasma. This fumigation might be sufficient to improve plant growth like in the case of nanobubbles [137]. Although fumigation had a positive effect on plant growth, plasma application had a stronger effect which may be due to the transport process being more efficient i.e., speed up the process by not relying on diffusion or provide more directionality. This highlights the presumably overlooked importance of oxygen especially considering that Rahman et al. [73] saw also more obvious changes in growth parameters when using an oxygen admixture instead of air.

This principle could likewise work for nitrogen gas but instead of modifying respiration, it may be directed toward other cellular processes such as photosynthesis since it is a major component of chlorophyll or protein synthesis [138]. As mentioned in the paper

of Gao et al. [52], the presence of CO and O₂⁺ signals confirmed that chemical etching of the seed surface by plasma played an important role in stimulation of seed germination [139]. These chemical changes may then be responsible for changing the biochemistry and molecular events in the plant and therefore, these will be discussed in the next section.

Biochemical and Molecular Factors

Chemical Species

RONS and Seed Coat Interactions

Regardless of whether the changes to the seed coat surface might loosen an elicitor such as oligosaccharins, as mentioned by Iranbakhsh et al. [78], many authors are in agreement and speculate that it is principally reactive oxygen and nitrogen species (RONS) that trigger biological processes.

Oxidation of the seed coat is very often observed but this can be propagated internally since there can be an increase in malonaldehyde (MDA), a product of lipid peroxidation, after plasma treatment as seen by both Los et al. [57] and Cui et al. [55]. This may be among the first steps in the signal transduction considering that lipid peroxidation does not rely on enzymatic activity, which is very limited in dry seeds [140].

Mujahid et al. [44] mentioned that it may be instead the hydroxyl radicals which are responsible for the cell wall loosening. Bafoil et al. [61] calculated an increased expression of 23 genes for class III peroxidases after plasma treatment, which are proteins localized in the seed coat which regulate concentrations of hydrogen peroxide and precede the rupture for germination. Pauzaite et al. [23] also suggested that ROS may alter the seed coat pigmentation, which is known to be linked to germination. The flavonoid biosynthetic pathways and abscisic acid, a hormone for dormancy, are regulated by the same gene locus. Although they had changes in the seed coat flavonoids, they could not find any clear connection in their study between flavonoids and seed germination parameters.

Others have seen that the seed coat pigmentation does in fact influence seed permeability and the rate of imbibition where brown seeds had faster water uptake, reached a germination optimum sooner but were more susceptible to imbibition damage than black seeds [141]. Liu et al. [56] also attempted to decipher between seed types using PAW and brought up in their discussion that seed storage proteins are typically oxidized during germination, which may facilitate the mobilization of the storage reserve. Therefore, it may be possible that plasma-derived ROS may be affecting the seed pigmentation first and then downstream the germination rate. Additionally, considering that Mueller et al. [142] suggested that ROS play a role in the cleavage of cell wall polymers, it may be that changes inside the seed in turn modify the outer layers. The mechanical pressure on the endosperm needs to be relieved for the radical protrusion but this is based on cell wall loosening, which is linked to the action of ROS [140] and this, again, may be another argument that external seed coat erosion might not be necessary for modifying germination.

Alternatively, it could also be that chemical modifications to the seed coat, for example through lipid oxidation, may lead to

the carbonylation of proteins, rendering them more susceptible to cleavage and leading to the breakdown of aleurone layer [140, 143]. Therefore, post-translational modifications, such as carbonylation and sulfhydryl group's oxidation, are also another mechanism by which ROS, specifically H_2O_2 , can shift a seed from a dormant to non-dormant state as shown by Oracz et al. [144] and Valderrama et al. [145].

ROS Entry and Involvement in Seed Development

Generally, it is not fully understood how external ROS are detected and how these signals are transduced in seed cells but this process may partly depend on the presence of water. Water is needed to trigger germination and increase respiration, a reaction which oxidizes sugars to release energy in the form of ATP. During respiration, ROS are produced as by-products and thus, ROS generation is the hallmark from dormant to metabolically active seeds [140]. Where the moisture content is low, there is very little, if any, enzymatic activity but there may be hydrated pockets within the seed, permitting limited metabolic activity. It could be that this pocket of water may assist the diffusion and retention of ROS in the seed and, therefore it may be that plasma-derived ROS accumulate in these pockets and trigger signaling for intracellular programs. This process may be done more efficiently with hydrated instead of desiccated seeds due to the higher water content. Nevertheless, in dry conditions, ROS may have an effect that is simply paused until imbibition [140] and this may be why there are long-term effects [23] or why long-term storage of plasma-treated seeds can still have a positive effect on growth parameters relative to the untreated seeds [102]. On the other hand, the effects of the plasma treatment may be continuously ongoing but are not morphologically obvious until imbibition and subsequent growth. Mildažiene et al. [128] pointed out that biochemical changes continue to occur in seeds at various levels, including hormonal balance, gene expression, oxidative processes, mRNA content, and protein translation during storage and these changes may occur across all of these levels after plasma treatment.

Although it is not known which ROS is/are responsible for the effect and how it/they enter, it is known that seeds have pores whose size is genetically regulated and this also may assist the diffusion of ROS into the seed [126]. H_2O_2 can interact with the surface and diffuse through the membrane but charged species such as superoxide are not able to bypass the membrane and are dependent on voltage-dependent anion channels called porins, which are only found in the mitochondria [146]. Despite its charge, superoxide can break down into hydroxyl and singlet oxygen and these may be able to bypass more easily [147]. In some cases, RONS bypass the membrane using aquaporins, protein channels used for water transport [148]. Transport also depends on the life stage of the plant since ozone can be taken up through the stomata in the leaves. Seol et al. [149] observed an accumulation of ROS in chloroplasts, and suggested that through the micropores, ROS can travel down further into the plant tissue, from the epidermis into the mesophyll but if too potent, chloroplast degradation occurs.

Considering the lifetime and complexity of the reactive species reactions, there is a bias for researchers to measure longer-lived species like H_2O_2 , O_3 , and NO and therefore, most of the focus for this section will be dedicated to these species herein [150].

Ozone

Surprisingly, little has been done to monitor and measure ozone during plasma treatments and it seems that many overlook the effect of ozone on seed germination despite it being possible to enhance germination with optimized treatment parameters. On the one hand, ozone can impair plant growth by replacing CO_2 and reducing photosynthesis. This is done by inhibiting the opening of the stomata due to the reduced flow of potassium ions [151]. In some cases, plants like mung beans are not able to overcome ozone stress with their antioxidant defenses [152]. On the other hand, ozone has been used to enhance seed germination [153] or improve fruit quality [154]. Ozone seemingly has an ambivalent role that is dependent on the concentration and length of treatment [155] as it is the case for many other treatments i.e., hormone, nanoparticles, heat. The authors mentioned that there is a variable response to the same ozone treatment based on the species and it is weak and transient. By using electron paramagnetic resonance (EPR), they showed that O_3 increased the concentration of radicals (carbon and oxygen species) in all tested species except one.

Pawlat et al. [72] measured 0.01 ppm of ozone produced during plasma treatment and had an effect on the growth parameters but it is not clear whether this is due to ozone or other treatment parameters, such as the short heat treatment at $40^\circ C$. Perhaps this ozone treatment might not have been sufficient, in terms of concentration and exposure time but is a good example to point out that it would be helpful to include as a control in studies to clarify whether the effect is due to ozone, other reactive species or other parameters.

It is especially interesting to differentiate this because ozone can trigger the production of ethylene, which then breaks down abscisic acid, the seed dormancy hormone [156]. Alternatively, it could be that ozone generates short-lived species inside the seed, which may be recognized as a signal for germination since the accumulation of ROS and peroxidation products is linked with seed dormancy alleviation [144]. As Sudhakar et al. [157] pointed out, the production of hydrogen peroxide is observed in the early imbibition period of tomato seeds and nitric oxide, hydroxyl radicals and superoxide radicals accumulate during seed germination in different species. For this reason, many scientists speculate that H_2O_2 and NO are the reason for the observed effects using plasma treatments, whether or not it is the short-lived species such as superoxide, hydroxyl and NO that are eventually converted into H_2O_2 [55].

Wang et al. [83] used a nitrogen plasma in open air and suggested that nitrogen oxides, which are known to have a role in dormancy and germination signaling, are present after plasma treatment and may initiate these biological processes [158]. Instead, Puac et al. [159] looked at meristematic cells of carrots treated with a RF plasma for <2 min and suggested that at least H_2O_2 and superoxide can pass through the cell membrane and reactive species may be one mechanism

since they observed fluctuations in levels of redox quenching antioxidant enzymes such superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), which control and limit damage from excessive levels of ROS. This was also observed by Henselova et al. [160] in maize using a DSCBD for <2 min. Simultaneously, these antioxidative enzymes may behave like sensors to detect ROS availability and redox perturbations so that an organism can respond appropriately [145, 161]. There is also an overlapping relationship between these enzymes, NO and H₂O₂ where NO positively regulates APX1 through a post-translation modification, S-nitrosylation, which then enhances resistance to oxidative stress and improves immune responses [162] and NO regulates itself as well as ROS [145, 163].

NO and H₂O₂

Rahman et al. [73] suggested that plasma induces H₂O₂ formation, which is found in hydrated seeds and is involved in imbibition and early germination. They compared Ar/O₂ to Ar/air admixtures and observed higher concentrations of H₂O₂ with Ar/O₂ without inducing scavengers that counter H₂O₂ production. They concluded that plants treated with this admixture had better growth parameters due to the increased H₂O₂ concentration and did not see any changes in NO. Likewise, after plasma treatment, an increase in H₂O₂ concentration was correlated with positive effects on germination, whereas a decrease was correlated with negative effects on germination [23]. The same authors also showed for the first time the oscillatory dynamics of H₂O₂, which occurs in *Arabidopsis* and conifers but it is not characteristic for other seed types such as radishes and sunflowers. This already suggests that there can be differences between species including on a molecular level.

Kang et al. [39] interestingly did not see an effect and observed high variation in rice germination. Los et al. [57] also saw no changes in H₂O₂ levels in wheat but still had growth enhancement. This suggests that there are either differences in the plasma that do not necessarily lead to changes in H₂O₂ and requires optimization, or that seeds respond differently, and it is not exclusively due to H₂O₂ but instead to nitrites and nitrates.

This latter point was heavily emphasized by Billah et al. [40] who observed an increase in H₂O₂ but think that nitrogen is the main contributor for enhanced growth in gram seeds. In contrast, Liu et al. [56] compared different gases using direct and indirect plasma treatments to produce PAW and soaked a variety of seeds. They were tempted to believe that effects are more likely due to oxygen-derived species. Interestingly, NO can downregulate the signal for H₂O₂ and will activate genes for antioxidant enzymes as pointed out by Iranbakhsh et al. [118] so once again, it is difficult to separate the effects of both H₂O₂ and NO.

In the case of H₂O₂, it is considered a long-distance signaling molecule, which is highly interconnected with hormones, metabolism and gene transcription. The signaling likely includes MAPK cascades as pointed out also by Babajani et al. [59]. ROS mediated signaling includes calcium signaling, protein phosphorylation and gene transcription which are redox sensitive. The relationship between ROS and MAPK is not fully elucidated and both are able to regulate each other.

These complexes phosphorylate transcription factors, kinases, phosphatases or other proteins, which can then change enzyme activity or gene expression [164].

Additionally, ROS may produce changes in calcium signaling and use different signatures in terms of duration and amplitude depending on the species and this will dictate what happens downstream, for example root elongation [165]. It was shown by Cui et al. [55] that there was increased calcium in the roots of 4-day-old *Arabidopsis* seedlings which were previously plasma-treated as seeds and they mentioned this may eventually lead to plant growth if maintained at a low level. Since there is little evidence about signaling due to plasma treatments, the focus now will shift from signal transduction to how hormones, metabolism and gene expression are modified with plasma, starting first with hormones.

Hormones

It is difficult to differentiate between the action of ROS and hormones because ROS are highly interconnected with hormones like salicylic acid (SA) and jasmonic acid (JA), which are widely reported. Information remains scarce with auxin and cytokinins, which are hormones that affect germination properties [150]. Nevertheless, “hormones modulate the effects of ABA/GA balance: auxin IAA (indole-3-acetic acid) is a negative regulator of germination; ethylene, cytokinins, brassinosteroids, and strigolactones can stimulate germination; SA and jasmonate (stress hormones) may affect germination positively or negatively depending on the situation” [53].

There are authors like Kitazaki et al. [110], who agree on the importance of reactive species. Specifically, they think it is the relationship between ROS and the hormones, which stimulates plant growth. It is true that the importance of hormones cannot be overlooked considering that the seed coat is a source of hormones for the developing seed [166, 167]. Mildažiene et al. [85] also demonstrated how a dry seed undergoes subtle metabolic modulation by using proteomics. They showed that vacuum affected the auxin/cytokine balance, cold plasma increased GA, and EMF decreased the amount of ABA and increased IAA and SA without changing GA despite not being able to make a clear connection between phytohormones and germination kinetics. Ji et al. [168, 169] also observed an increase in GA in spinach seeds but did not measure any other hormones. The increase in GA may be the result of plasma-derived ozone [157] although it is often speculated that it is specifically auxin and cytokinins that are affected, which are hormones that increase and stimulate cell division, proliferation and elongation. Perez Pizá et al. [170] showed that with plasma treatment, there was a decrease in ABA and increase in IAA, a hormone which increases growth by regulating enzyme activity. They also detected H₂O₂, which coincided with an increase in ethylene after 24 h of imbibition.

It may be that plasma-derived ROS regulate hormone production while for example increased auxin levels may be the reason for increased lateral root growth as pointed out by Wang et al. [171] where the authors correlated increased levels of auxin in tomato with lateral root growth under drought stress. Stolárik

et al. [104] found changes in auxin and cytokinins with a 2-min plasma treatment in peas. They found an increase in IAA and oxIAA as well as zeatin, the most common cytokinin, and correlated this with increased growth parameters. This is logical since these two hormones work together; auxin is responsible for DNA replication and initiating the cell cycle whereas cytokinins trigger cell division and mitosis [172].

It seems that plasmas may somehow modulate concentrations of hormones and there may be a link with auxin especially considering that this hormone also affects xylem differentiation [173]. It has been observed that plasma treatment modified the diameters of root and stems as well as the differentiation of tissues such as xylem and phloem [51, 52, 58, 174]. These changes in root morphology may then enhance nutrient exchange [68] which was also proposed by Zahoranová et al. [97]. Moreover, Babajani et al. [59] pointed out that auxin transport may also be affected by NO, which is often produced in plasmas. Additionally, it could very well be the case that auxin biosynthesis is upregulated because it is known that abiotic or biotic stresses increase the shikimate pathway which produces the precursor for IAA.

Metabolism

As stated previously, there is a link between hormones and metabolism and both primary and secondary metabolism, which are involved in growth and defense, respectively, are altered after plasma treatment [175].

Regarding primary metabolism, increased ATP levels along with ethanol were observed, suggesting increased anaerobic respiration [92]. Moreover, higher concentrations of protein and sugar were observed by Islam et al. [64] and Billah et al. [40] due to an increase in reserve utilization enzymes. Billah et al. [40] explained that this could be because H_2O_2 transduces the signal for soluble sugar synthesis and therefore, more soluble sugar and protein are seen after plasma treatment [62]. Moreover, exogenous treatment with H_2O_2 can stimulate germination by breaking dormancy through the oxidative pentose phosphate pathway, which provides reducing power and carbon for the new growth [176]. This pathway also links primary and secondary metabolism because it provides the precursor for the shikimate pathway, which is important for plant defense.

Regarding secondary metabolism, an increase in enzymatic antioxidants like catalase [58], superoxide dismutase [78], phenylalanine ammonia lyase (PAL) and peroxidases [59] as well as non-enzymatic antioxidants like total soluble sugar and proline to better tolerate stress have been observed, likely due to the increased concentration of ROS. Furthermore, Ghasempour et al. [43] showed an increase in phenols, chlorophyll, flavonoids and alkaloids with plasma treatment. Pauzaitė et al. [23] has seen changes in flavonoids after plasma treatment while others have observed increased phenolic compounds [45, 168, 177].

Defense

ROS may also trigger defense compounds which can originate from the shikimate pathway and phenylpropanoid pathway to induce the production of precursors. For example, H_2O_2 can activate the shikimate pathway [178, 179]. ROS can also make the plant readily available in a redox state to respond quickly

to stress as stated by Filatova et al. [45]. Iranbakhsh et al. [118] suggests that the defense response, triggered by ROS and/or UV, modulates the hormone balance since they saw an increase in PAL, a key enzyme in the phenylpropanoid pathway. This pathway also produces protective proteins called pathogenesis-related proteins and depending on whether they are acidic or basic, they can be upregulated by salicylic acid and ROS or methyl jasmonate and ethylene, respectively [180].

Although Perez et al. [181] used PAW, they looked at several genes involved in plant defense in an infected tomato plant and saw an increase in the gene expression of *pal* (phenylalanine ammonia lyase) but not *pr1a*, *pr4*, *pr5* (pathogenesis related protein) or *erf1* (ethylene response factor). The gene *pal* is involved in the phenylpropanoid pathway and makes defense compounds like phytoalexins and phenolic compounds and therefore, this information complements the increase in phenolic compounds seen experimentally by others previously mentioned in the section Metabolism.

Gene Expression

ROS can also affect gene transcription either directly or indirectly through hormone conjugates as mentioned by Stolárik et al. [104]. Redox sensitive transcription factors are widespread among animal, bacteria and plants [147] and these factors can be modified through the formation of disulfides upon sensing ROS [140].

Unsurprisingly, there are others who think plasma also modifies gene expression although molecular information concerning plasma-seed treatments is very limited. Hayashi et al. [182] suggested that ROS generated in plasma with water vapor may be a method to control the redox state of the plant by changing the thiol quantity (oxidizing cysteine to cysteine with OH radicals). This has an important role in gene transcription and therefore can change the plant response.

Iranbakhsh et al. [38] observed an increase in the transcription factor WRKY1 and other enzymes involved in secondary metabolism in plasma-treated hemp seeds. WRKY is of particular interest since it is a family of transcription factors involved in many biotic and abiotic stress responses such as fungus, cold stress, salt stress, and drought tolerance. Furthermore, they are known for regulating phenolic compounds and there are specific factors such as AtWRKY23 that regulate auxin. Moreover, there are also interactions between MAPK cascades and this WRKY family and they can also activate PR proteins [183].

The other genes that have been studied were by Guo et al. [91] who observed an increase in LEA chaperone during stress, Ji et al. [168] who saw increased expression of a hydrolytic enzyme called pullulanase in spinach seeds, Ghasempour et al. [43] who saw an increase in gene expression for DAT, an enzyme in the biosynthesis of vinblastine and vincristine, alkaloids with anti-cancerous properties and Islam et al. [64] who showed changes in gene expression of ascorbate peroxidase and catalase but not superoxide dismutase with an air plasma in rapeseed.

These few preliminary studies demonstrate that plasma treatment can change gene expression for both primary and secondary metabolism, for growth and defense, respectively.

Epigenetics and Genetics

These changes by the plasma treatment in the short-term may be due to epigenetics such as regulating DNA cytosine methylation, which inactivates gene expression [74, 184].

Zhang et al. [92] checked the methylation of genes involved in ATP synthase, an enzyme needed to produce energy for the cell, and TOR kinase, an enzyme which may increase metabolism and biosynthesis for energy and biomass production, and saw decreased methylation, meaning that the expression of these genes increased. Nevertheless, it cannot be ruled out yet that there may be changes to the DNA considering that genotoxic effects from plasma treatment have been observed [185].

Although it was not verified, Mildažiene et al. [85] found many similarities between cold plasma and electromagnetic treatment in protein expression but this may also be done epigenetically or through post-translational modifications. Despite the authors attributing the changes to radiation, it may be the action of hydroxyl radicals or other ROS since they too are produced from high energy radiation [186]. Additionally, there also remains the possibility that instead the DNA repair process is triggered by for example ozone and this may be responsible for the improvement in germination kinetics [187, 188].

Lastly, the plant genome itself may play a role in sensitivity to plasma treatment. Kobayashi et al. [47] treated *Arabidopsis* seedlings and saw that the ecotypes Col and *Ler* responded differently to the same plasma treatment although the results were not statistically significant. Lo Porto et al. [67] also pointed out that asparagus germination is strongly influenced by ecotype although they did not include this in their study. Therefore, the genetic component should not be overlooked when considering plasma-seed treatments and studies should be done on multiple generations since plasma treatment can have long-lasting effects in the same generation as observed by Sarinont et al. [102] where the growth enhancing effects remained even after 17 months of storage of plasma-treated radish seeds.

In summary, it remains difficult to infer whether these effects are primarily attributed to the action of a single mechanism like mechanical scarification, chemical modifications, or changes in biochemistry through ROS; even within ROS, each species behaves and functions differently. Additionally, variables such as the state of dehydration or hydration of the seed may influence the interaction and retention of ROS.

Ozone specifically in the presence of UV radiation may undergo reactions to eventually generate superoxide and hydroxyl radicals in the seed coat or these short-lived species may directly interact with the seed coat and this could be the critical point that determines how the external physical and chemical stimuli are transformed into internal biological stimuli.

The seed coat pigments can be altered and seed coat embedded enzymes like superoxide dismutase, NADPH oxidases or peroxidases can transform these species into signaling molecules like H_2O_2 , which can more easily diffuse through the membrane or the apoplastic space, and then transduce this signal either through secondary messengers like calcium and MAPK cascade or be transmitted without the assistance of enzymes. Once the signal is sent, the hormonal balance may be modulated

between GA and ABA to break dormancy, to increase auxin and cytokinin to accelerate the germination process, and increase ethylene, SA and JA for stress or disease resistance.

In parallel, metabolism may be modulated through the addition of water and enhanced gas exchange to modify enzyme activity to break down food reserves but at the same time, increase enzymatic and non-enzymatic antioxidants to shield against this sudden burst of ROS either externally derived or from metabolism. As a result of this stressful stimulus, metabolism in other defense pathways like shikimate and phenylpropanoid may be then activated to produce precursors in anticipation of future stressful events such as hormones or protective proteins.

CONCLUSION AND FUTURE OUTLOOK

What has been shown to date is a combination of plasma device geometries, treatment methods and seeds that are able to alter the plant parameters. On the one hand, this diversity emerges from individual researchers considering what is relevant for their society and local economy, but on the other hand, this also makes it difficult to standardize the current research. We seem to have reached a point where there is potential in this technology as a proof-of-concept although there may be an inherent bias by publishing solely positive results, giving the impression that finding these setups is simple and it only takes trial-and-error to optimize the treatment conditions. Therefore, it would be helpful for the readers to also publish negative results to know what is not working when designing these treatments to move toward standardization and improve our fundamental understanding.

Most scientists are using DBD plasma enclosed in a chamber with air as the process gas although there is flexibility in choosing the type of plasma device. Air plasma is practical and produces a rich chemistry. However, the role of humidity in these plasma-seed treatments is still debated. Is it best to work with dry or wet seeds? Should one control and add or remove humidity, for example, by a gas flow?

Many authors reported evidence, more often than not, that plasma treatment modifies the seed surface in such a way that water uptake increases; this is either done by poration, removal of the topmost layers or through oxidizing the surface to improve the water interaction. It is not yet clear whether it is through mechanical, chemical means or both and whether this is dependent on the plasma treatment, seed type or both. How much energy needs to be injected into the plasma to obtain these effects? To address this, future studies should continue correlating surface modifications with changes in germination in a systematic manner and clearly record the electrical characteristics. This would clarify if mechanical erosion is necessary to induce a change, under which circumstances mechanical erosion or chemical alterations are needed, and specifically which gas types and electrical properties are needed.

It also seems that most authors agree that RONS are predominantly responsible for the observed plant growth effects. However, it is not yet clear whether it is ROS, RNS or the synergistic action of both. It is also not clear if it is purely a RONS effect because plasma is a synergy of individual mechanisms.

Although most authors agree that the effects are not due to heat, it remains difficult to define temperature in these studies, especially in the presence of a gas flow. Is the seed temperature after treatment, the plasma temperature or the temperature of the device measured? Is it certain that an increase of a few degrees is not enough to trigger a heat shock response? Is the relative humidity altered by the plasma heating? For this reason, it would be useful for scientists to include controls in their studies for heat, ozone, electric fields, and humidity, mimicking what they are using in the plasma treatment where possible.

Most authors observe changes at the molecular level although these studies are still extremely limited. More studies focusing on gene and protein expression would at least provide insight about whether the same genes are activated across different plasma treatments and across different seed types. It is also not clear whether these effects are long-term and at which point they would be considered genotoxic or adverse for plant growth. The bottleneck here will be that gene expression studies are limited to already sequenced plant genomes. However, these results may be applicable to closely related species.

As a next step, it would be useful to understand how each parameter in the plasma treatment affects the outcome so it is more predictable to be able to control the output. To accomplish this, it will require the continued collaborative efforts of biologists, chemists and physicists and these standardized protocols will likely need to be tailored to the seed type due to the diversity in the seed coat and build on the information from industry or associations such as AOSA (Association of Official Seed Analysts) where plasma is an added parameter.

Much of the outcome of the plasma-seed treatment seems to depend on both the plasma setup and seed features. If the seed has many layers that need to be scarified, plasma may help with mechanical erosion through etching or by melting the wax with the heat produced as a by-product of plasma generation. If the seed is rather permeable, it may functionalize the surface through the addition of chemical groups on the surface to become more hydrophilic and enhance gas exchange to then affect the seed biochemistry. Therefore, it may be that there are several modes of plasma treatment that can be selected i.e., if you need mechanical scarification and erosion, then use high power AC and argon for ion bombardment, if you need a gentle dose with ROS for chemical modification of seed coat, use nanopulse power for better ROS generation and lower temperature, or if you want to generate NO or H₂O₂ or if you want to delay or accelerate germination for storage or sowing, respectively, choose the appropriate gas type.

Very little has been done in terms of economic analysis other than by Niemira [189] but it would be useful to mention explicitly

the power density of the device, the maximum number of seeds that can be treated to have an effect and potentially disclose the cost of manufacturing the plasma device to then see which designs would be easiest to implement and scale-up. This does not mean one plasma device is used universally as one of the advantages is the flexibility in design so people can adapt their treatment to their surroundings (seeds may vary in their value or importance depending on the country). By understanding the plasma-seed interactions and mechanisms, this will also help with setting up regulations around this technology since it is still ill-defined.

Generally, future studies should ideally correlate results using methods from different fields as far as possible, such as combining material science techniques with biological analysis and recording plasma parameters to find trends across experiments. The most urgent questions are: which treatment parameters are necessary to see a reproducible beneficial effect on seeds, can these parameters be applied to a plethora of seeds or is it necessary to tailor them to each seed type, how is the plasma treatment affecting the seed on a molecular level, is it possible to have these plasma treatments and biological effects consistently reproduced, can the plasma treatment be reliably scaled up for industrial applications, and how does plasma treatment compare to already existing methods such as acid or mechanical scarification? Provided that scientists now focus on the molecular effects of plasmas, with time, we might understand in detail how plasma-seed treatments work to develop this into a viable seed processing technology. Our hope is that plasma treatments will be another technology useful to the agriculture community.

AUTHOR CONTRIBUTIONS

AW conceptualized the review and figures, performed literature search, designed the figures, and wrote the manuscript. IF and AH read and approved the manuscript. All authors contributed to the article and approved the submitted version.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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GLOSSARY

Glossary of abbreviations (in alphabetical order).

Abbreviation	Full name	Short description
ABA	Abscisic acid	Hormone known for its role in maintaining dormancy and for inhibiting germination
AC	Alternating current	Usually in the kHz range in these applications
APX	Ascorbate peroxidase	A H ₂ O ₂ scavenging enzyme found in plants to protect the cell from damage by H ₂ O ₂ or OH radicals
AtWRKY23	Auxin regulation factor	Auxin-inducible gene and member of WRKY transcription factor family involved in growth and development, biotic and abiotic stress, and signal transduction
auxin IAA	Indole-3-acetic acid	IAA is the most abundant form of the hormone auxin; auxin is involved in cell elongation, cell division and differentiation, phototropism, geotropism
CAT	Catalase	Enzyme which catalyzes the decomposition of H ₂ O ₂ to water and oxygen; protects from oxidative stress
CCP	Capacitively-coupled plasma	A continuous discharge maintained in a gas by AC voltage between electrodes
DAT	Acetylvindoline O-acetyltransferase enzyme	An enzyme involved in the biosynthesis of vindoline, a precursor of vinblastine and vincristine
DBD	Dielectric barrier discharge	Electric gaseous plasma between electrodes, of which at least one has a dielectric (insulating) surface layer
DSCBD	Diffuse coplanar surface barrier discharge	A type of dielectric barrier discharge
EDX	Energy dispersive X-rays	Analysis of X-rays after sample irradiation by high energy electrons
EMF	Electromagnetic fields	Electric and magnetic fields; pulsed, or low frequency (kHz) or high frequency (GHz)
EPR	Electron paramagnetic resonance	Analysis of electron spin by excitation and detection
erf1	Ethylene response factor	Gene encoding a protein belonging to the ERF transcription factors, one of the largest groups involved in biotic and abiotic stresses using a hormone ethylene
FTIR	Fourier-transform infrared absorption spectroscopy	Absorption spectroscopy suitable for identifying polar molecules
FTIR-ATR	Attenuated total reflectance FTIR	Absorption spectroscopy suitable for the surface of opaque samples
GA	Gibberellic acid	Hormone produced to trigger germination
HSPs	Heat shock proteins	Proteins produced when cells are exposed to temperatures above their normal growth temperature; can also be triggered by oxidative stress, toxins, heavy metals
JA	Jasmonic acid	Hormone involved in wound response, which can be inflicted by herbivores, and systemic acquired resistance
LEA	Late embryogenesis abundant protein	Proteins associated with seed development and involved in responding to abiotic stresses such as desiccation and cold stress
MAPK(KK)	Mitogen-activated protein kinase cascade	Major signal transduction pathway in eukaryotes composed of several proteins called kinases which take extracellular stimuli and convert into cellular responses; activity altered with the addition of a phosphate group (phosphorylation); can regulate plant development, growth, ripening, hormone signaling and in response to biotic and abiotic stresses
MDA	Maldonaldehyde	A product of lipid peroxidation
NADPH (oxidase)	Nicotinamide adenine dinucleotide phosphate (oxidase)	Co-factor involved in oxidation-reduction reactions, protects against ROS, regenerates glutathione (GSH) (membrane-bound enzyme which generates superoxide or H ₂ O ₂)
NTP	Non-thermal plasma	Plasma in which the electron temperature far exceeds the gas temperature
PAL	Phenylalanine ammonia lyase	Catalyzes first reaction of phenylpropanoid pathway which is involved in polyphenol biosynthesis (flavonoids, lignin, phenylpropanoids); belongs to secondary metabolism used for plant defense
PAM	Plasma-activated media	Any liquid, or other medium, exposed to plasma activation
PAW	Plasma-activated water	Water exposed to plasma treatment
PR proteins	Pathogenesis-related proteins	Proteins induced upon pathogen attack; part of systemic acquired resistance
pr	Pathogenesis-related protein	Gene encoding for pathogenesis related protein
RF	Radio frequency	Alternating voltage, generally from 1 MHz to 300 MHz
RNS	Reactive nitrogen species	Reactive radicals containing nitrogen, such as nitric oxide, for example
RONS	Reactive nitrogen and oxygen species	Any combination of ROS and RONS
ROS	Reactive oxygen species	Reactive radicals containing oxygen, such as ozone, superoxide, hydroxyl radicals
SA	Salicylic acid	Hormone synthesized in response to pathogens; part of local and systemic acquired resistance; induces PR proteins
SDBD	Surface dielectric barrier discharge	Dielectric barrier discharge between electrodes disposed on a surface
SEM	Scanning electron microscopy	Electron microscopy suited to surface analysis
SOD	Superoxide dismutase	An enzyme which catalyzes superoxide into H ₂ O ₂ and oxygen

(Continued)

GLOSSARY | Continued

Abbreviation	Full name	Short description
TOR kinase	Target of rapamycin kinase	An enzyme which may increase metabolism and biosynthesis for energy and biomass production according to nutritional, hormonal or other cues
UV	Ultra violet radiation	100–400 nanometer wavelength, including UV-A, UV-B and UV-C regions
VDBD	Volume dielectric barrier discharge	Dielectric barrier discharge in a gas between electrodes
WRKY1	Transcription factor	Family of transcription factors involved in many biotic and abiotic stress responses
XPS	X-ray photoelectron spectroscopy	Analysis of high-energy electrons after sample irradiation by X-rays
μ -XRF	Micro X-ray fluorescence	Fluorescence of X-rays from a sample bombarded by high energy radiation