

Review

Changes Induced in Seeds as a Result of Non-Thermal Plasma Treatment in Plasma Agriculture Applications

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Abstract

Non-thermal or cold plasma is an innovative agricultural technology used for the treatment of seeds, producing physicochemical and biochemical changes without thermal damage and stimulating germination and plant growth. The interaction of reactive species generated in cold plasma modifies the morphology of the seed surface, increasing porosity, producing microcracks, removing material or producing other physical changes, and chemically modifying it. The changes induced positively influence the rate, speed, and uniformity of germination, as it is believed that these changes take place as a result of activated metabolic pathways, regulated hormone balance, and stimulated production of enzymes involved in the mobilisation of nutrient reserves needed for seedling growth. Plasma sources, electrical parameters, feed gas, and processing time are some of the essential factors involved in tuning the effects on seeds. Optimising the outcomes and their adaptation for specific species is crucial to maximise the benefits and avoid inhibitory effects. In the frame of ecological and sustainable agriculture, with the benefits given by cold plasma, this review follows the modifications produced by different sources on the seeds, starting from morphological changes to biochemical ones, up to germination, aiming to facilitate the understanding of the interaction and outcomes. We also address the challenges, including variability of biological responses, the need for standard procedures and parameters, and development of scalable technologies. A thorough examination of the changes induced in seeds as a result of non-thermal plasma treatment not only facilitates the improvement of experimental designs and reproducibility but also plays an important role in advancing seed treatment technologies and, ultimately, enhancing crop yields in a sustainable manner.

Keywords: plasma agriculture; non-thermal plasma; cold plasma; seeds modification



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1. Introduction

Plasma agriculture is an emerging research field, consolidated in the past decade, based on the abilities of cold or non-thermal (NTP) plasmas to trigger various positive outcomes after the treatment of a biological medium [1–4]. The range of possible applications expanded due to the complexity of NTP plasma and its properties among which the ability to process temperature-sensitive materials is crucial. Especially when produced in

atmospheric air, cold plasma is a powerful chemical reactor owing to the multitude of reactive species that are created. As a result, NTP treatments are complex, the reactive species being accompanied by the electric and magnetic field, as well as radiation produced in the discharge. This makes NTP a versatile tool for seed treatments, disinfection and disease control of seeds, plants, water, soil, and post-harvest products, and fertilisation [4–19]. Being nonchemical, in gas phase treatment technology is user- and environmentally friendly and can be considered a green technology. It not only promotes healthier plant growth but also increases resistance to pests and pathogens, offering a sustainable alternative to traditional chemical treatments that often pose environmental risks. Using NTP in seed treatment is particularly significant in the context of increasing global food demands, with an urgent need for environmentally friendly agricultural practices. Traditional seed treatments usually involve harmful chemicals that can have a negative impact on the ecosystems, creating lasting pollution. In contrast, NTP treatments present eco-conscious solutions, minimising toxic residues while enhancing seed performance without the environmental burden associated with the conventional methods [17]. Moreover, NTP can inactivate microbial loads, addressing seedborne diseases—a persistent challenge in agriculture and the food industry [13,18]. As the agricultural sector is increasingly seeking sustainable alternatives to traditional chemical practices, NTP stands out as a promising solution with its capabilities ensuring its relevance in addressing future food security challenges [19].

The synergistic effects of all plasma components can trigger different outcomes, positive or negative, the latter being less reported, to the detriment of science, and figuring out the insights into the processing mechanisms. Among the positive effects disinfection—NTPs being well known as disinfecting agents even before the development of plasma agriculture applications, stimulated germination the seed dormancy can be broken much easier in some cases, enhanced growth of the plants the growth speed, number of roots, plant vigour can be improved, stimulation production of nutraceutical compounds secondary metabolites production is enhanced in some cases, and improved tolerance to stress plants are less prone to be affected by different abiotic stresses such as drought or salinity [4–14]. At the same time, some plasma treatment conditions can inhibit these processes, being too intense and stressful for plants to handle. Reported effects include damage of the processed seeds, reduced germination, inhibition of plant growth, and production of secondary metabolites [20–22].

The insights into the mechanisms responsible for all these effects are far from being completely figured out, owing to NTP complexity on one hand and, on the other hand, due to the different responses of different plant species. The common denominator in all situations seems to be the reactive species that not only change the surface of the seeds, influencing their properties (especially those related to the behaviour relative to water), but also induce biochemical changes that trigger secondary processes during plant growth. Based on this, we believe a crucial step in understanding and reproducing the positive outcomes of NTP treatments of seeds is to understand what happens at the seed level during and soon after seed processing. To do that, we followed the literature reports related to the physicochemical modifications of the seeds' surfaces (analysis of seed surface morphology and chemical composition), hydrophilicity connected with the water uptake capacity, biochemical modifications, and germination.

2. Bibliometric Evaluation of the Relationship Between Relevant Research Fields and Non-Thermal Plasma Treatment for Seeds

A bibliometric analysis of keywords was performed using the VOSviewer software (software version 1.6.20), based on scientific publications related to non-thermal plasma (NTP) treatment for seeds [23]. The selected dataset comprised a total of 1134 publica-

tions retrieved from the Web of Science Core Collection, using a set of relevant search terms including “SEM seed”, “Low-temperature plasma”, “NTP effects on seed surface”, “germination parameters”, “microbial decontamination”, “plasma agriculture”, “seed germination enhancement”, and “SEM seed surface plasma agriculture”. Figure 1 illustrates the keyword co-occurrence network generated from the dataset, analysing papers published since 1978, which is in fact everything found on the Web of Science within the previously mentioned limitations. In this network, nodes represent individual keywords, with their size proportional to the frequency of occurrence within the analysed literature. The links between nodes indicate co-occurrence relationships, referring to how often two keywords appear together in the same publication. The proximity of nodes reflects the strength of these associations—keywords that co-occur more frequently are positioned closer together in the network [24,25].

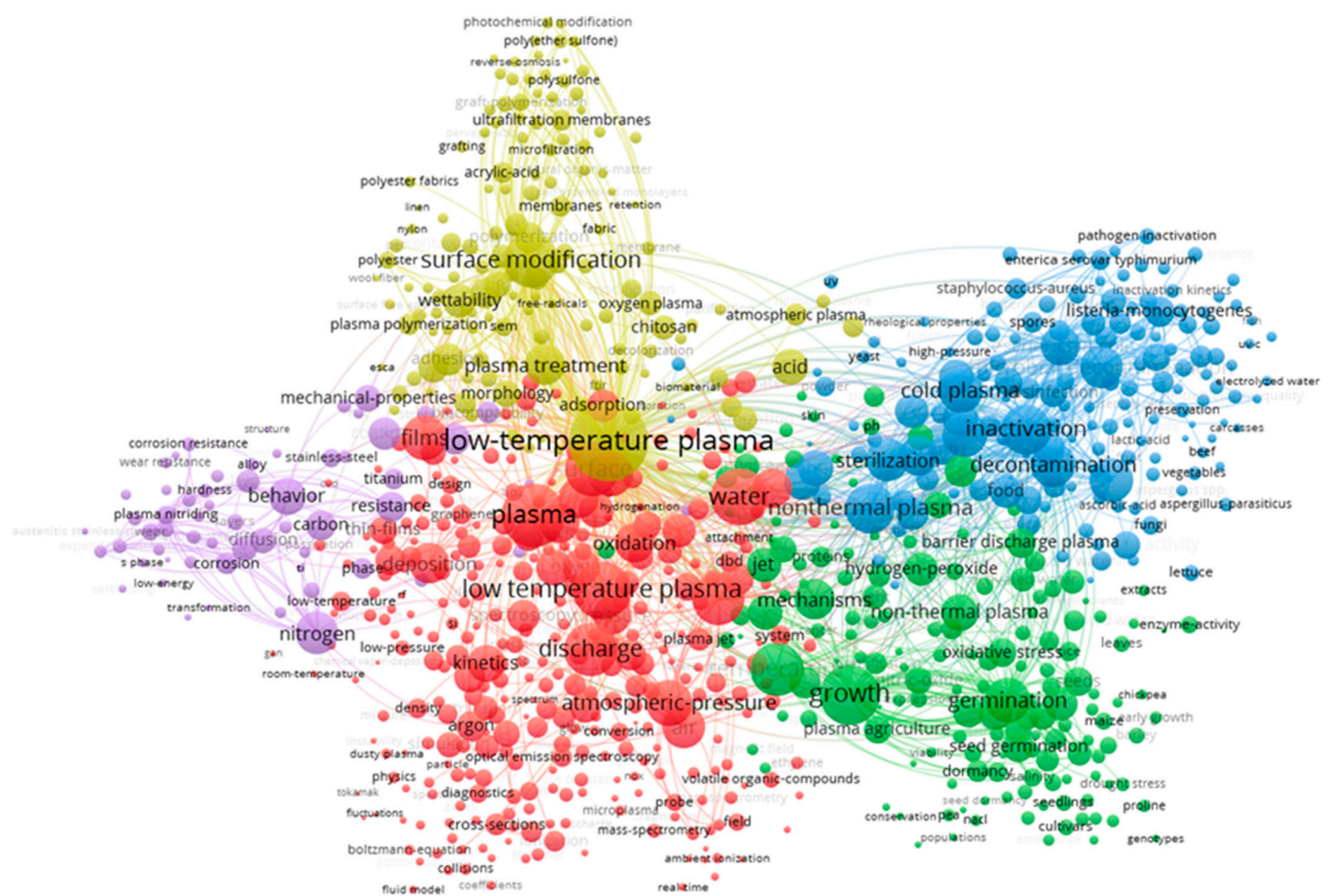


Figure 1. Co-occurrence network of keywords related to NTP seed treatment based on Web of Science articles (VOSviewer visualisation). The node size represents the frequency of occurrence, while the proximity of the connecting lines reflects the strength of association between nodes. The colour coding corresponds to their respective thematic clusters. The overlapping in the figure does not affect its scientific understanding.

The bibliometric analysis conducted with VOSviewer underscores the central importance of non-thermal plasma (NTP) treatment for seeds within the broader field of plasma research. The visualisation was created through a co-occurrence analysis utilising the full counting method. In VOSviewer, the recommended normalisation method is association strength, which balances the weight of co-occurrences by considering the overall frequency of each term. This approach mitigates the bias of widely used keywords and highlights more specific and meaningful relationships within the network. To enhance interpretability,

a minimum threshold of six keyword occurrences was set and 22 keywords unrelated to the study focus (e.g., textiles, dyes, and nanomaterials) were excluded. This refined process allowed the analysis to emphasise the significance of plasma-based technologies in agriculture, particularly in seed treatment and crop improvement. The bibliometric map displays four main clusters, all interconnected through the concept of “low-temperature plasma.” However, the blue cluster, related to “germination,” “growth,” “oxidative stress,” and “seed treatment,” stands out as particularly notable. This cluster illustrates how NTP has become a key focus for sustainable agricultural practices, with consistent evidence of its role in improving seed germination, promoting seedling vigour, and enhancing resistance to abiotic stress factors. Keywords such as “emergence,” “seed germination,” and “non-thermal plasma” confirm the strong scientific interest in applying plasma directly to seeds as a cost-effective, nonchemical technology to boost crop productivity. The green cluster complements these findings by linking plasma research to “inactivation,” “decontamination,” and “microbial control.” This is directly relevant for seed safety, as plasma treatments have demonstrated the ability to reduce microbial load on seed surfaces without damaging their viability. Such results are particularly significant in pathogen management contexts, where plasma could serve as a non-toxic alternative to chemical disinfectants. By coupling microbial inactivation with enhanced germination capacity, NTP seed treatments provide a dual benefit: safer seeds and stronger early-stage growth. The red cluster continues to represent the physical and chemical mechanisms behind plasma generation and discharge.

While not directly related to agriculture, terms like “plasma discharge,” “air plasma,” and “gas” support the technological optimisation of plasma sources. Advances in understanding these mechanisms are vital for designing NTP systems that can be applied efficiently in agricultural settings, from laboratory experiments on seeds to large-scale seed treatment facilities. Meanwhile, the yellow cluster, centred on “surface modification” and terms such as “plasma treatment” and “polymeric surfaces,” illustrates that NTP research in materials science shares significant methodological similarities with agricultural seed treatment. Just as plasma alters the surface properties of polymers, it also modifies the seed coat, increasing hydrophilicity and permeability. These physical modifications of the seed surface are among the primary mechanisms explaining improved germination rates and uniformity following plasma exposure. A smaller purple cluster addresses microstructural effects in metals and corrosion studies. While not directly related to seeds, this cluster highlights the broad interdisciplinary scope of plasma research and the transfer of knowledge across different domains. This analysis clearly positions non-thermal plasma seed treatment as a rapidly growing area within plasma science.

The strong connections between germination, growth, oxidative stress mitigation, and microbial decontamination demonstrate that NTP offers unique advantages in agriculture. By enhancing seed performance while simultaneously reducing microbial risks, NTP provides a sustainable, chemical-free approach that directly contributes to food security and agricultural resilience. This centrality in the network analysis indicates that future research will likely continue to expand NTP applications for seeds, bridging fundamental plasma science with real-world agricultural practices.

3. Non-Thermal Plasmas Used for the Treatment of Seeds

Non-thermal or cold plasmas can be classified according to several criteria. A first criterion is related to the energy balance: cold plasmas are not in thermodynamic equilibrium, with low ionisation degree and lower electron densities than hot plasmas, ions have a much lower temperature than electrons, near room temperature. Another relevant criterion relies on the mode of plasma generation. Typical sources include discharges produced at atmospheric pressure in different configurations, such as dielectric barrier

discharges (DBDs), atmospheric pressure plasma jets (APPJs), corona discharges, gliding arc, each having different characteristics in terms of operational mode, delivered power, and properties, such as density of reactive species. Generally, the devices can use only atmospheric air or, especially in the case of plasma jets, feed gas such as helium, argon, or different mixtures. This carrier gas influences the chemistry of the plasma, determining the production of the reactive species. Plasma jets are discharges produced between two electrodes, followed by plasma transport to the exposed target by means of the feed gas [5,26–29]. The concentrations of reactive species reaching the target are lower than for the direct sources, such as in the case of DBD, where plasma can interact directly with the exposed material. DBDs in surface or volume configurations are frequently used in agriculture due to their ability to produce a variety of reactive species combined with UV radiation and intense electric field at atmospheric pressure without the need of complicated equipment [2,3,8,11,30–42].

Except for these atmospheric pressure discharges, low-pressure configurations have been used for seed treatments. These have advantages, such as the ability to control the density and type of reactive species, by using a specific gas, but imply the use of more sophisticated equipment, owing to the need for a vacuum chamber [29]. Such low-pressure discharges can be produced using radiofrequency or microwave systems.

Non-thermal plasma generation initially involves the production of free electrons as a result of applying a strong electric field to a gas. The accelerated electrons interact with the neutral molecules and atoms, producing secondary ionisations, excitations, and molecular dissociations, which lead to the formation of a complex mixture that includes positive and negative ions, metastables, free radicals, ultraviolet, and visible photons, making NTP a powerful chemical reactor. This provides NTP with sufficient chemical potential to initiate reactions on organic surfaces, without requiring massive heat transfer, and enables physicochemical modifications, thereby synergistically contributing to changes in the seed coat.

The type of plasma source considerably influences the biological response. For example, streamer corona discharges or plasma jets have the advantage of targeting individual seeds or small batches, while DBDs ensure a more uniform application over a larger surface, being suitable for technological scale-up [3,11]. DBD also has a high efficiency in plasma agriculture due to the intense production of a large variety of reactive species and UV radiation. In this context, seeds exposed to a DBD discharge can experience visible physical changes, such as cracks or increased porosity [1,3]. DBDs can operate in ambient air, but their performance can be adjusted using gases such as oxygen, rare gases (e.g., helium, argon), or mixtures [43]. The choice of gas determines the profile of the reactive species produced: oxygen increases the ozone concentration, nitrogen favours the formation of reactive nitrogen species, each having a different role on the outcome of seed treatment [5,44]. The physical configuration of DBD systems can vary considerably. Standard design involves two electrodes separated by a dielectric layer, but there is a multitude of adapted configurations for discharge uniformity and scalability. An example is the diffuse coplanar surface barrier discharge, where the electrodes are integrated on the sides of a ceramic plate, which allows plasma generation in ambient air [34]. Another variant is the surface DBD with flexible electrode, helpful in treating seeds directly or placed inside a package [39]. The choice of the configuration depends on the geometry of the biological target and treatment outcomes, balancing uniformity and localised energy consumption. DBDs are suitable for bulky or irregular seeds, which can be directly placed in the active zone of the discharge without complex manipulation systems or expensive vacuum chambers [10]. DBDs are also easier to implement in agriculture for large-scale

treatments, have a good operational stability and low operational costs especially when associated with industrial-scale implementation compared to other plasma sources.

Innovative configurations have been developed to increase the efficiency of seed treatments and reduce the potential of seed damage by precisely controlling the discharge parameters and uniformising the discharge. A relevant approach consists of the use of hybrid systems that combine streamer corona discharges and dielectric barrier discharge, creating structures that are capable of combining the advantages of both methods [45,46]. In such a configuration, the dielectric layer acts as a current limiter and prevents the formation of arcs, while the specific sharp electrodes generate local intense fields that have the role to initiate ionisations in the gas. This allows a uniform exposure of the samples. Configurations using double plasma sources have been proven effective in limiting the local temperature and producing more uniform treatments [38]. There are also unconventional electrode configurations; geometries such as gliding arc electrode or corona discharges have been explored, creating concentrated plasma zones that are able to induce intense biochemical responses, including enzymatic activation and increased antioxidant enzyme activity [35].

The treatment efficiency is not only determined by the plasma source, but also by other parameters such as electrical properties of the discharge, gas composition, and treatment time [34]. Table 1 presents some of the most common devices, along with the most important findings following seed treatment. Not only do the plasma type and processing parameters determine the outcome but also the seed species. Thus, adaptations and optimisations are necessary in each case and for every targeted outcome to avoid inhibitory and negative effects.

The reactive species produced inside NTP were proven to be crucial in the destruction of microbiological loads from the surface of agricultural products such as seeds, plants, fruits, etc. The most important seem to be those containing oxygen (e.g., O_3 , O^+ , OH^+ , H_2O_2) highly reactive, that can have both physical and chemical interactions, producing etching and changing the structure or destroying chemical bonds of important biomolecules (e.g., oxidation of lipids, enzymes, proteins, DNA damage). Nitrogen reactive species must also be considered, with NO_x being very important. Due to these effects, NTP is also suitable for removing toxins or other harmful chemical components, such as pesticides, from the treated surfaces, or even food allergens, contributing to the reduction in protein allergenicity [47].

Among the parameters monitored during the seed treatments, there are electrical characteristics (discharge current, voltage, power), radiative species identified from the optical emission spectra, and radicals. The discharge power controls the energy transferred to electrons, which dictates the ionisation and excitation processes in the working gas and the rates of formation of RONS. However, the relationship between discharge power and the biological effects is not linear. The power settings are essential depending on the plasma source. In DBD configurations that operate at atmospheric pressure, the increase in voltage might lead to the intensification of the discharges and expansion of the uniformity of active discharge zones [11]. In APPJ, power variations modify the length of the jet and the rate of energy transfer towards the surface. In the case of corona and hybrid discharges, power adjustments influence the spatial distribution of the electric fields, concentrating areas rich in reactive species. The optimisation of discharge power must be correlated not only with the duration of the treatment but also with the distance between the active electrode and the seed surface. When scaling up the discharge for industrial purposes, the adaptability of the sources to maintain a constant power uniformly on the treated area becomes critical for the reproducibility of the treatment outcomes. Modern systems integrate optical sensors that monitor the emission spectrum of the plasma and automatically adjust parameters to maintain optimal conditions [45].

Table 1. Typical types of non-thermal plasma used lately for seed treatment: feed gas used, processing time, discharge power and/or power density, type of seed, effects related to seed modification and the corresponding reference (missing information from the table was not found in the respective references).

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
Cold plasma	Nitrogen Helium Air Oxygen		25 W	Mung bean	- enhanced germination (air, oxygen) - no significant change in hydrophilicity - cracks and etching (air plasma)	[48]
LFGD	Air Air/oxygen		60 W	Wheat	- increased water uptake - surface etching	[49]
RF plasma	Air	120 s	6.8–18 W	Pepper (<i>Capsicum annuum</i> , Roni-272)	- no change in surface morphology - increased hydrophilicity	[50]
FEDBD DBD	Helium Air	15 min		<i>Arabidopsis thaliana</i>	- ruptures of testa - etched seed surface	[51]
DBD	Air Argon	3–81 min		Cotton	- improved water uptake - increased cold tolerance	[33]
RF low pressure	Nitrogen	3–15 min	10 W	Artichoke (<i>Cynara cardunculus</i> var. scolymus)	- small cracks and holes that increase with processing time	[52]
HV nano-second pulsed plasma		1–5 shoots		Spinach (<i>Spinacia oleracea</i>)	- increased hydrophilicity - no change in water uptake	[53]
q	Helium/air	10–300 s	30 W	Nasturtium (<i>Tropaeolum majus</i>)	- increased hydrophilicity - increased water uptake - no significant FTIR changes - increased O/C - no significant surface changes	[54]

Table 1. Cont.

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
DCSBD	Air	30–300 s	400 W 80 W/cm ³	Maize (<i>Zea mays</i> L. cv. Ronaldinio)	- increased hydrophilicity - surface functionalisation (C=O-, O-H, N-H, C-N) - no degradation of surface - increased water uptake - disinfection	[13]
LPDBD	Ar/oxygen Ar/air	90 s	45 W	Wheat	- increased H₂O₂ in seeds - decreased NO in seeds	[55]
FEDBD	Air	15 min		<i>Arabidopsis thaliana</i>	- resistance to saline stress	[31]
DBD	Air	0.5–10 min	2.5 W	<i>Arabidopsis thaliana</i>	- etching of the surface - shrinkage to detached epidermis - improved activity of antioxidant systems	[56]
Plasma jet	Argon	1–10 min		Fenugreek	- etching of seed surface - increased germination	[57]
DBD	Air	30, 60, 180 s		Wheat	- stimulated germination for short treatments - decrease in WCA down to 0 - no visible micro modification	[58]
Plasma jet	Air	1–10 min		Tomato (<i>Solanum lycopersicum</i>)	- destroyed testa - affected trichomes	[44]
RF plasma	Argon	1–15 min		<i>Moringa oleifera</i>	- etching of the surface - increased hydrophilicity	[59]
AC corona	Air			Alfalfa	- increased hydrophilicity - increased water uptake - cracks	[60]

Table 1. Cont.

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
LPRF DBD Plasma jet	Argon Air Argon	2 min 30–120 s 15 s/seed	75, 100, 125, 150 W 75, 100, 125, 150 W 0.41, 0.51, 0.61, 0.72 W	Sunflower	- slight roughening (LPRF) - increased hydrophilicity (more for low pressure plasma)	[29]
DCSBD	Air Oxygen Nitrogen	30–300 s	400 W 80 W/cm ³	Pea (<i>Pisum sativum</i> L. cv. Prophet)	- oxidation of lipids and polysaccharides - appearance of some structures on the surface - highest water uptake in nitrogen plasma	[61]
DBD	Air	3–30 min	3.05 W/cm ²	Radish	- no changes of the surfaces	[30]
DBD	Argon	10–60 s	53.5 mW/cm ³	Wheat Barley	- altered surface properties - increased hydrophilicity - incorporation of hydroxyl, carboxyl and carbonyl groups for wheat	[32]
RF plasma	Argon	1–20 min		Flax	- erosion, microroughening, perforations, cracks - increased hydrophilicity	[62]
DBD	Argon Ar/oxygen	10 min		Dehisced ginseng (<i>Panax ginseng</i>)	- disinfection	[8]
RF plasma Afterglow	Oxygen	5–30 s	200, 600 W	Wheat (<i>Triticum aestivum</i> L. Apache and Bezostaya 1)	- stronger etching for plasma - presence of debris	[63]

Table 1. Cont.

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
RF low pressure	Oxygen	0.3–120 s	50, 300 W	Alfalfa (<i>Medicago sativa</i> L.)	- increased hydrophilicity - etching, erosion, cracks - rougher surface - increased O/C	[64]
LPDBD	Argon/air	3 min		Maize	- increased roughness	[65]
RF plasma	Argon	3–4 min		Rice	- increased water uptake - fungus inactivation	[18]
Plasma jet	Argon	1–15 min	1.2 W	Mung bean	- increased hydrophilicity - cracks, effects increasing in time	[28]
DBD	Argon Nitrogen Oxygen Carbon dioxide	1–5 min	83.28 W upper electrode 5.28, 9.12, 12.86 W lower electrode	Beetroot (<i>Beta vulgaris</i>)	- increased surface roughness - enhanced porosity, cracks - increase in O containing functionalities - increased water uptake	[38]
DBD	Air	1–15 min	5.3 W	Barley (<i>Hordeum vulgare</i> L. var. planet)	- reduction in contamination - increased water uptake - increased roughness - increased surface damage - small increase in CO_s groups - increase O/C	[40]
SCP DBD	Argon/air	30–120 s		Rice (<i>Oryza sativa</i> var. <i>Indica</i> cv. KDML105)	- increased hydrophilicity	[45]
RF plasma	Air	180 s	50 W	Wheat	- etching of the surface	[17]

Table 1. Cont.

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
LFGD	Argon/air	30–120 s		Maize (<i>Zea mays</i> L.)	- fractures of the surface	[66]
RF low pressure	Oxygen/water	60 s	10, 80 W	Bambara	- increased hydrophilicity - etched seed surface - increased porosity	[67]
Plasma jet	Argon	30 s–30 min		Basil	- etching and cracks	[26]
Plasma jet	Argon	5–120 s		Spring wheat	- increased hydrophilicity - seed erosion - increased surface energy	[27]
DCSBD Plasma jet	Air	15–45 s	400 W 30 W	Soybean	- no noticeable surface changes - attachment of polar oxygen groups	[34]
DBD Gliding arc (afterglow)	Air	20 min	1.06 W 4.23 W	Rice	- increased hydrophilicity - smoothing of the surface - cracks	[35]
DBD	Air	2–15 min	5–5.4 W	Melon	- increased roughness - development of wrinkles	[36]
Cold plasma		4 min	100 W	<i>S. leriifolia</i>	- disruption of the seed coat structure	[68]
DBD	Air	30–120 s		<i>Brassica oleracea</i> <i>Lepidum sativum</i>	- strong etching - exposure of internal layers (broccoli) - improved hydrophilicity - increased roughness (cress)	[3]

Table 1. Cont.

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
LPDBD	Air	2–8 min	10 W	Eggplant (<i>Solanum melangena</i> L.)	- increased smoothness vs. time - increased water uptake	[69]
jet kINPen 11	Argon	10–20 s		Fenugreek	- folded surface, strong etching - increased roughness - increase in O/C ratio - exposed K and Ca	[70]
DBD	Air	20–100 s		Mung bean	- increased conductivity of seeds - increased hydrophilicity - small cracks on the surface	[37]
DBD	Air	30–120 s		Alfalfa	- strong etching - cracks, residues - decrease in hydrophilicity	[39]
DBD	Air	30–120 s		Fenugreek	- stimulated germination for pre-soaked seeds - less etching for direct plasma, stronger modifications for intensified radicals - increased hydrophilicity	[2]
DBD	Argon	30–420 s	100 W	Iranian soybean cultivars	- minor alterations of the seeds for small treatment time - altered morphology for long time treatment (cracks, pores)	[41]
DCSBD	Nitrogen Air Oxygen	30–120 s	400 W	Soybean (<i>Glycine max</i> L.)	- increased hydrophilicity - no chemical changes (FTIR)	[71]

Table 1. Cont.

NTP	Feed Gas	Treatment Time	Discharge Power/Power Density	Seed	Effects	Reference
Cold plasma	Helium Oxygen Argon	30–150 s	100–500 W	Peanut	- fine cracks, small holes - damage increased with discharge power - depolymerisation of macromolecules (Ar plasma)	[72]
DBD	Ar	60, 120 s	80 W	<i>Momordica charantia</i> L.	- some transcription genes were affected	[73]
RF plasma	Air	15–90 min	50 W	Maize Wheat Barley psyllium	- increased roughness (maize, wheat) - deposits on the surface - strong etching (90 min)	[74]
RF plasma	He/air	15 s		Rapeseed <i>Brassica napus</i> L.	- increased plant resistance to stress	[75]
RF plasma	Air	1–3 min	0–100 W	Cowpea	- increased surface energy - gradual increase in surface roughness, cracking, exfoliation	[76]
DBD	Air	6–10 min		<i>Prosopis koelziana</i>	- resistance to saline stress	[42]
SCP DBD	Air Ar/air	5–15 min		Chinese kale (<i>Brassica oleracea</i> var. alboglabra)	- localised etching and disrupted microstructure (SCD) - uniform surface roughness, broader structural modifications (DBD) - disinfection	[11]

The treatment time is a critical parameter which directly determines the threshold between positive and inhibitory effects. Many studies observed a non-linear behaviour of the analysed parameters with increasing time. Long processing intervals could lead to visible deterioration in the embryo and the reduction in its viability [42]. The optimum processing time is determined by the dynamics of physicochemical processes induced by the interactions of plasma components with the seeds. The increase in hydrophilicity saturates after some time; for example, in the case of mung beans, the contact angle remains unchanged for treatments longer than 4 min, even if the germination rate still increases, up to 10 min of treatment, due to hormonal changes that continue [28]. This difference between the saturation of physical effects and the continuation of biochemical changes implies that the optimum processing time should be evaluated on many levels, not only related to the morphological changes. The seed structure considerably influences the sensitivity to the exposure time. Seeds with thin testa of highly permeable hilum succumb faster to plasma-induced stress; in this case, short treatments are recommended to prevent damage that could inhibit germination and growth. Those seeds with thicker testa might require longer processing, giving more time for the reactive species to pass through the physical barrier and initiate the desired changes in the seed. To identify these particularities, it is necessary to observe physiological markers of stress, such as the appearance of morphological abnormalities in roots or hypocotyls immediately after germination [77]. Excessive treatments not only affect the morphology of the seeds but also change the direction of physiological responses. If short treatments function as moderate oxidative stress, stimulating the expression of antioxidant genes, prolonged exposure to NTP might generate severe distress, inhibiting key enzymes responsible for the mobilisation of nutrients [13].

The temporal evolution post-treatment should also be considered: the induced changes remain only for a limited time. For example, the “ageing” process is similar to what happens in the case of NTP treatment of polymers, where hydrophobicity progressively returns for long storage time. Thus, it is possible that after some time the treated seeds may lose their abilities if not sown within a short time [67]. To this extent, plasma treatment should be correlated with both treatment time and duration until cultivation.

Optimum processing intervals are dictated by the NTP. Large DBDs allow the maintenance of a uniform delivery of plasma even for large processing intervals [32], while APPJ action is concentrated in a small area, especially if the exposure is too long relative to the gas flow rate and flow gas composition [29].

Each agricultural species has an optimal time window, which can be determined by correlating morphological outcomes, chemically measurable parameters (e.g., concentrations of reactive species), and physiological responses (e.g., germination rate) with processing time intervals [78].

The feed gas used to produce the NTP has a decisive influence on the composition (types of species and densities) of reactive species, implicitly determining the interactions with the seeds and physiological responses. The choice of the feed gas determines the concentrations of the reactive oxygen and nitrogen species and their behaviour [32]. The use of an inert gas such as argon or helium has the role of stabilising discharge and maintaining uniformity at low voltages. However, to generate biological effects, it is essential to have a reactive gas, such as oxygen or air, capable of producing radicals [63]. Used as a carrier gas, ambient air provides RONS with synergistic effects: ROS oxidise organic components of the testa, while RNS act as intracellular redox messengers modulating hormonal responses [34]. Comparative experiments have revealed that the use of oxygen can stimulate germination more by increased concentrations of ozone and hydroxyl radicals. In contrast, argon produces more moderate effects due to the reduced chemical reactions; its

impact is derived, rather, from facilitating the formation of secondary reactive species when mixed with reactive gases, either in feed mixtures or with the surrounding atmospheric air [5]. When used as a feed gas, nitrogen supports the production of nitrogen reactive species, such as NO, recognised for its ability to regulate gene expression involved in antioxidant and hormonal metabolism [32].

Overall, when an inert gas is used, it is necessary to control the ratio between oxygen and nitrogen added as feed gases. For wheat treated in DBD, the germination increased differently as a function of the feed gas: 24% with air, 28% for nitrogen, and 35.5% with argon, indicating that the physical nature of the stabilised discharge in an inert gas can produce effects at least comparable, if not higher, than those obtained without it [79]. The outcomes of the treatments when using different feed gases are different. Prolonged treatments with air or oxygen as feed gases often lead to visible cracking due to strong oxidative reactions [41]. The use of an inert gas not only limits the erosion effects but also reduces the rate of subsequent oxidative processes.

The interaction between NTP and the seeds is complex due to the many components: electromagnetic field, charged particles, radiation, and radicals. During discharge, electrons and ions hit the seed coat, producing local physical etching and microerosion [1]. Radicals produce chemical etching, removing material from the surface. The topographical changes include the formation of pores, cracks, and other modifications that we shall discuss in detail in another section. The changes in the surface can change the water behaviour of the testa and sometimes penetrate into internal structures [80]. UV radiation induces photochemical changes. The high-energy photons can directly break chemical bonds in the organic molecules from which the surface is made. These fragmentations of the polymeric structures of the testa facilitate the further interaction of plasma components and oxidative reactions.

Despite maintaining a low local temperature, the areas where the action of plasma is intense can exhibit a rapid increase in temperature for small areas and short times, which promote structural and spontaneous molecular rearrangements [59]. Some radicals can introduce functional groups onto the surface of the seed, such as hydroxyl, carbonyl, and nitro, that increase the surface energy of the testa and change the water contact angle [80–82]. Some reactive species not only produce direct oxidations but also penetrate the testa barrier to the endosperm and embryo [83].

4. Modification of Seed Surfaces as a Result of NTP Treatment

NTP treatment of seeds can be strong enough to induce physical changes. These can be evidenced using scanning electron microscopy (SEM) or atomic force microscopy (AFM) of the outer part of the seed, called testa. SEM offers the possibility of analysing the detailed surface morphology changes induced by plasma components such as charged particles, reactive species that hit the surface, producing physical and chemical etching, just as it happens for any other inert material processed in plasma. Chemical changes can be detected with methods such as X-ray photoelectron spectroscopy (XPS) or energy-dispersive X-ray spectroscopy (EDS). These physical and chemical modifications may change the hydrophilic character of the seed surfaces, making it possible to further dictate some effects starting from germination to plant growth. It is also connected to the water absorption rate. All these aspects are essential, and we shall analyse them in this section. Figure 2 presents the most important aspects related to the modification of seeds following NTP treatment.

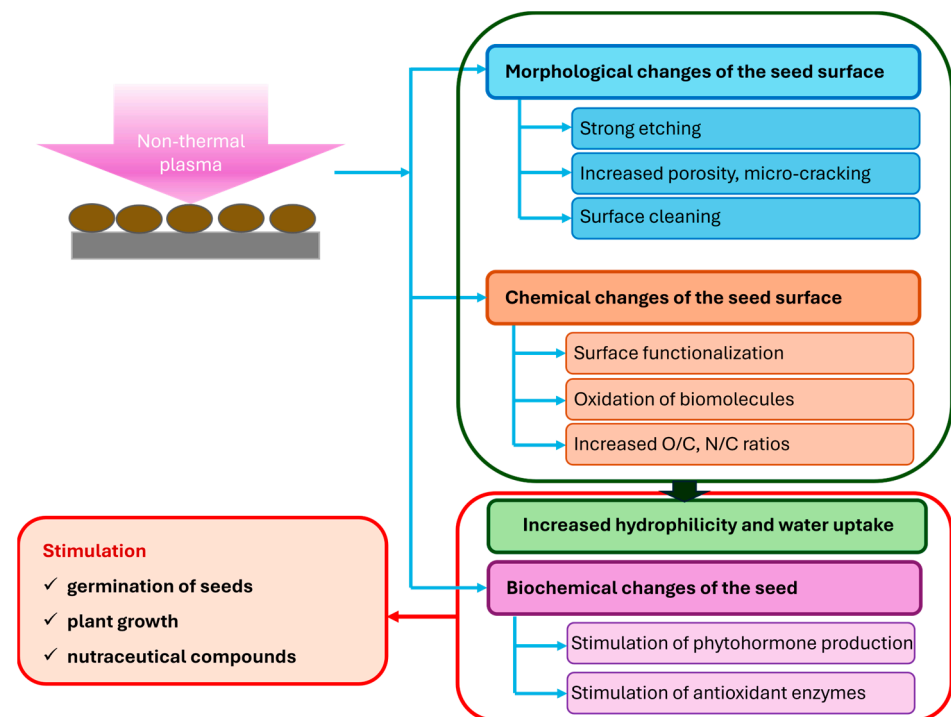


Figure 2. Schematic representation of the most important aspects of NTP treatment of seeds discussed in this paper.

Plasma-generated reactive species attack the seed surface layer, partially removing hydrophobic structures (e.g., waxes) and creating micro-fissures. This leads to an increase in hydrophilicity, as evidenced by a decrease in the water contact angle, indicating faster water absorption. It also increases seed surface permeability due to enlarged cracks and pores, which facilitate water and oxygen penetration, accelerating germination [3,37]. Plasma-induced morphological changes reduce germination time and increase resistance to water stress. Differences between species and technologies highlight the need for customised protocols [28]. We shall detail some of the most important changes in seeds reported in the studied literature.

4.1. Morphological Changes Evidenced Using Scanning Electron Microscopy (SEM)

The structure and topography of the seeds' surfaces treated with NTP are profoundly influenced by the combined action of reactive species, local electric fields, charged particles, and UV radiation emitted by the NTP. The physicochemical etching can sometimes lead to the cleaning of the surface, with decreased roughness and removal of biological material, while sometimes it can increase the roughness through the production of pores, grooves, and microcracks. These changes significantly increase with the exposed area and create zones with high surface energy that favour the adsorption of water and nutrients after sowing. The surface modifications depend on the NTP used, discharge gas, power, and processing time. Mild exposure produces moderate etching with fine pitting, without destroying the integrity [26,38]. As the time and/or the applied power increase, the changes become more pronounced, with deep cracks, exfoliation of the outer layers, and even carbonisation of the organic material [76].

Figure 3 shows the results of an DBD treatment of two seed species: broccoli (Figure 3a–d) and cress (Figure 3e–h). For the same discharge voltage, one can see that as the processing time increases from 30 to 90 s (Figure 3f,g) the etching removes material from the surface, which becomes smoother. When increasing the discharge voltage (Figure 3b–d) with the same processing time, large cracks appear and the destruction of

the cell wall is apparent. With cover, meaning keeping the reactive species closed to the samples (Figure 3e), there is also strong etching with material removal from the surface of the seed. On the other hand, the same processing conditions do not obviously modify the seed coat of cress (Figure 3h), showing that the outcome of NTP treatment strongly depends on the seed species probably due to the different structure and thickness of the seed coats as shown in Figure 3i–l [3]. Broccoli has a thinner coat (Figure 3i,j), while cress coat is made of several thicker layers (Figure 3k,l).

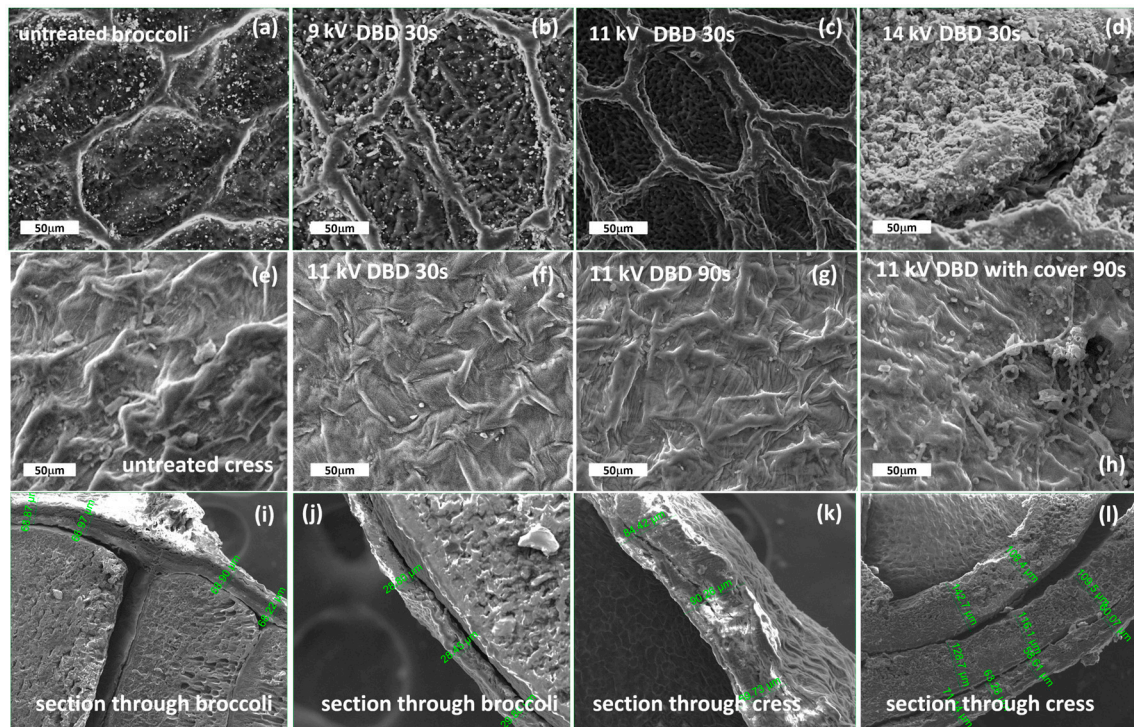


Figure 3. ESEM images of seeds surfaces for broccoli: (a) untreated, (b) 30 s in 9 kV DBD, (c) 30 s in 11 kV DBD, (d) 30 s in 14 kV DBD, and for cress (e) untreated seeds, (f) 30 s 11 kV DBD, (g) 90 s 11 kV DBD, (h) 90 s 11 kV DBD with intensified action of reactive species, (i,j) sections through a broccoli seed, (k,l) sections through a cress seed (adaptation from Motrescu et al., 2023) [3].

Disruption of the testa from tomato seeds exposed to air plasma jet was reported by Adhikari et al., with the partial breakdown of the outer layer and trichomes. Ahmed et al. found strong etching of Bambara seeds' surface after cold plasma treatment, which improved the hydrophilicity and water uptake [67]. In the same study, chilli and papaya seeds exhibited the same microstructural modifications, namely, pores were created as a result of plasma treatment.

The contact with reactive species, which is determined by the feed gas, makes a significant contribution to the surface modifications. The presence of oxygen enhances oxidative reactions that fragment cuticular polysaccharides and lipids, creating deep reliefs and hydrophilic areas [38]. In the case of nitrogen as feed gas, the degradation is slower, but NTP produces a granular texture that may retain its mechanical protection properties while increasing permeability [84]. When using argon in a plasma jet, treatments from 30 s to 20 min of basil seeds indicated strong peeling of the seeds' surface, increasing with processing time [26]. Electron microscopy results of various species show that the sensitivity of the surface is directly related to the chemical composition of the testa [81]. Seeds that are rich in lignin show increased resistance, requiring more aggressive processing [7]. In contrast, those with high content of polysaccharides respond promptly to moderate treatments, suffering disaggregation of the structural networks [85].

4.2. Water Contact Angle of Seed Surfaces

Topographic transformations are often correlated with measurable changes in the water contact angle of the seed surfaces. Its decrease indicates the increase in hydrophilicity, which can be determined by the combined effects of the introduction of polar groups and increased roughness [38]. Most research found an increase in hydrophilicity following NTP treatments of seeds. Usually, normal seeds have water contact angles greater than 90°. The exposure to NTP can considerably reduce the water contact angle, sometimes down to 0° [52]. Ahmed et al. found that the water contact angle of Bambara seeds reduces with time after seed treatment with cold plasma, similar to the behaviour of polymers processed with plasma, assuming that the reported effects could be due to the modification of lignin and cellulose [67]. Other research found that cold helium plasma treatment of six Chinese varieties of milled rice resulted in a significant improvement in hydrophilicity and increased water uptake, which leads to the reduction in cooking time [86].

Two mechanisms were suggested. One is related to the etching of the surface of the seeds, the other one to surface functionalisation, proven by chemical monitoring of the surface of the seeds by some spectroscopic method. The particle bombardment and UV photons degrade and restructure the lipid layer, exposing the polysaccharide matrix, and introducing polar groups such as hydroxyl and carbonyl [71]. The functionalisation of the surface changes the surface energy and reduces the water–solid interfacial tension. The etching amplifies the decrease in the contact angle according to the Wenzel model: the micro- and nanometric topography of the surface enhances the capillary effects in the microstructures. Studies show clear differences between the feed gas used and seed species. In the case of air, for example, more reactive species are produced than in the case of nitrogen or an inert gas, and the water contact angle decreases more sharply. ROS generate rapid oxidations leading to a pronounced reduction in the contact angle.

The correlation between microscopic changes (e.g., increased roughness, presence of cracks), chemical–functional changes (e.g., introduction of polar functional groups), plasma treatment parameters (e.g., power, feed gas, treatment time), and macroscopic responses (decrease in contact angle) outlines the image of a causal chain and demonstrates that the interfacial changes at the surface of the seeds is a very important factor through which NTP modulates the biological performances of the seeds [21,52,63,71].

Regarding the possibility of seed storage after processing, while keeping the properties resulting from plasma treatment, the few existing studies indicate some surface recovery, with a different increase in water contact angle, probably due to the differences between seed species and/or plasma sources used. Ahmed et al. conducted a detailed study of seed surface hydrophilicity change following plasma treatment. For Bambara seeds, they found an initial reduction in WCA from 114° to 44° with a slight recovery up to 69° after 60 days [67]. Gurgain et al. found a substantial decrease in the hydrophilicity of the fenugreek seed surface after 98 days of storage [70]. WCA increased from 56° to 108° for seeds treated for 10 s using a plasma jet, while for those treated for 20 s, the WCA increased from 31° to 94°. In all studied cases, the value after storage was still smaller than the one for untreated seeds, which was 121° [70]. An alternative method that can accompany plasma treatment and stimulate germination has been found to be pre-soaking the seeds, then treating them after the excess water is removed [2,73]. Pre-soaking the seeds is known to help initiate and speed up the germination process by softening the protective seed coat and hydrating the embryo, which is similar to what happens in moist soil after seeds are planted. The process is beneficial, especially for large and slow-germinating seeds with thick coats, facilitating water absorption. Compared to the dry seeds treated in the same conditions, the pre-soaked fenugreek seeds germinated almost twice as fast. At the same time, the sprouts produced were longer and with longer roots, with increased production

of chlorophyll pigments and other nutraceutical compounds, all effects being attributed to the intensified action of reactive species produced in an atmospheric pressure surface dielectric barrier discharge.

4.3. Electrical Conductivity

Ahmed et al. studied the conductivity change in Bambara seeds exposed to cold plasma, finding increased conductivity of treated seeds, with considerably higher values than those measured for untreated seeds [67]. The conductivity decreased in time, up to 60 days after the treatment. The authors also suggested that oxygen ions inside the plasma play an important role in the reported effects. The changes in seed conductivity are due to the effects produced by the reactive species that interact with the outer cell membranes, releasing intracellular electrolytes, simple sugars, or organic acids [67]. Moderate increases are associated with the stimulation of seed vigour, reflecting the balance between preserved structural integrity and the ability for the rapid mobilisation of nutritional reserves necessary for germination [64]. High conductivities are due to the massive release of cellular components due to the extensive rupture of the membranes; this leads to decreased viability and germination rate since some of the seeds will be dead. Thus, the evaluation of conductivity can serve as an operational threshold for the calibration of NTP treatments.

4.4. Monitoring of Seed Chemistry

The monitoring of the surface chemistry post-NTP treatment has been performed using spectroscopic methods. Energy-dispersive X-ray spectrometry (EDS) estimates the elemental composition of the analysed sample as percentages. Fourier transform infrared spectroscopy (FTIR), Raman spectroscopy, and X-ray photoelectron spectroscopy (XPS) give information about the chemical bonds found in the biomolecules from which the analysed surface is made of.

Studying the modifications of Bambara, chilli, and papaya seeds exposed to cold plasma, Ahmed et al. found an increase, as a function of time, in the oxygen compounds following plasma treatment, similar to other research on cold plasma treatment of biomolecules [67,87]. The process is mostly a post-treatment oxidation, similar with the ageing behaviour of polymers. Many other reports found an increase in oxygen-to-carbon ratio from XPS measurements [38,40,64,70], which is the result of the interaction of ROS with the biomolecules, involving the introduction of functional groups such as hydroxyl, carbonyl, and carboxyl [32]. For plasma produced in gases containing nitrogen, there is also an increase in nitrogen content due to the interactions produced by the RNS, which leads to the appearance of -NH and -NO_x functional groups [76].

EDS mapping of the NTP-treated surfaces can detect the distribution of other elements, such as minerals (K, Ca, Mg). These can be mobilised from the deeper layers or mobilised following the degradation of the polysaccharides that were stabilising them [40].

4.5. Modifications of Surface Chemistry Induced by NTP

In order to understand NTP processing of the seeds, a multilevel analysis is necessary; one crucial aspect involves determining the chemical modification at the level of the seeds surface induced by the treatments. XPS and EDS are two methods focusing on the atomic concentrations and types of chemical bonds present on the first couple of nanometres of the analysed surface [64]. The most common results reported indicate an increase in oxygen- and sometimes nitrogen-to-carbon ratios, most probably due to the interactions of RONS with the exposed biomolecules. The interactions of RONS with the surface lead to functionalisation with oxygenated groups (e.g., C=O, C-O) or groups containing nitrogen (-NH₂, -NO_x) [17,36,38]. The research even demonstrates that the changes can last even after long periods of time (up to 60 days) [67]. In NTP-treated seeds,

the vibration bands associated with O-H become larger and more intense, which indicates new hydrogen bonding between the newly introduced polar groups and water molecules. This phenomenon is correlated with the above-mentioned increased wettability and water uptake and increased polar character, facilitating the interaction with water.

The result of such functionalisation leads to an increase in the surface energy and reduced water contact angle. The increase in carboxyl functionality was evidenced to be associated with localised oxidation reactions in the areas rich in polysaccharides or aromatic lignin, a process that not only changes the polar behaviour of the surface but also leads to the appearance of chemically active sites where other compounds such as biostimulators or protective agents can attach [85].

Using several spectroscopic methods helps figure out the outcome of NTP treatment from the chemical point of view, confirming the introduction of several functionalities: stretching of C=O from carboxylic acids and amides detected in infrared spectroscopy becomes more intense, -CH aliphatic signals decrease due to the substitution of hydrogen with electronegative atoms from the generated plasma [53]. Using the FTIR, an increase in the absorption bands for O-H, N-H, and amide groups was also observed, confirming the presence of polar groups and a decrease in the signals for -CH₂ (lipids) [13]. Overall, the results indicate a simultaneous oxidation and nitrification process, governed by processing parameters. The feed gas and power dictate the type and concentrations of reactive species, while the treatment time governs the functionalisation, long processing presenting a risk for excessive depolymerisation. Monitoring the surface chemistry post-treatment is not only a static analysis but a good operational tool for calibrating the NTP treatments.

Hydroxyl, ozone, and hydrogen peroxide produced by some NTPs act as strong oxidation agents, promoting the cleavage of C-H bonds and oxidation of hydrocarbonate chains [78]. They can also generate unstable molecular fragments and accelerate chemical etching through the strong oxidation of lipids and proteins on the seed surface [72].

Plasma treatment was also shown to expose minerals (Si, K, Ca), which was attributed to the removal of the wax layer and the exposure of the underlying cellular structures [64,70]. The migration of such elements is probably due to the degradation of the polysaccharides stabilising them or through their mobilisation from deeper layers under the electromagnetic fields of the discharge [40]. These minerals detected on the surface of the seeds might have additional effects on the wettability and initial metabolic activation of the seeds.

4.6. Surface Decontamination of Seeds

Cold plasma (non-thermal plasma, NTP) has demonstrated high efficiency in removing contaminants from the surface of agricultural seeds, including microorganisms (bacteria, fungi) and pesticide/fungicide residues [7,82]. The main mechanisms by which plasma acts are as follows:

- Etching: Plasma removes contaminant layers through oxidative processes, breaking down organic and inorganic substances from the seed surface.
- UV Sterilisation: UV radian emitted by the plasma destroys the genetic material of microorganisms, reducing the microbial load.
- Introduction of Functional Groups: Plasma modifies the surface energy of seeds, creating hydrophilic groups (e.g., -OH, -COOH) that can reduce the adhesion of contaminants.
- Chemical Remediation: Plasma can break down residual pesticides or fungicides on the seed surface, transforming them into less toxic compounds.

Most studies conducted so far have focused on the antimicrobial inactivation or sterilisation potential of plasma treatments, particularly against bacteria and fungi with thick cell walls, which appear to be of primary interest. Research has mainly investigated

the effectiveness of plasma in reducing fungal species commonly associated with the contamination of stored cereal seeds (such as *Alternaria*, *Aspergillus*, *Botrytis*, *Mucor*, *Penicillium*, *Rhizopus*, *Sclerotinia*, and *Trichoderma*) [8,11,18,88].

An equally important contribution of plasma treatment lies in lowering the levels of aflatoxins produced by these fungi, a factor of major significance for enhancing food safety [7]. The experimental results presented by Hoppanova et al. indicate that low-temperature atmospheric pressure plasma generated by a DCSBD plasma source in ambient air can be successfully used for treating wheat and barley seeds with cold plasma, leading to a reduction in fungicide doses. The synergistic effect of treatment with fungicide and LTP used against phytopathogens on the surface of wheat and barley seeds was more effective [7].

Structural alterations induced by cold plasma in microorganisms are strongly influenced by cell type and the composition of the cell wall. In bacteria, Gram-positive species such as *Kocuria* tend to be more susceptible, largely due to the relatively simple and less protective structure of their cell walls. In fungi, cell wall components such as chitin and melanin provide a degree of resistance by limiting oxidative damage; however, this protection is only partial. Reactive oxygen species (ROS) generated during plasma exposure are capable of penetrating the cell wall and inducing multiple forms of cellular damage, including lipid peroxidation, protein oxidation, and nucleic acid degradation. As a result, even fungal species with more complex protective structures, such as *Coniochaeta*, can be effectively inactivated when ROS overcome these defence barriers [8].

It is difficult to compare different studies because the types and parameters used for plasma generation are quite different. Additionally, the effects of various treatments on various seed types and in various environmental conditions must be taken into consideration. It is evident from studies conducted up to this point that the effectiveness of various treatments on the decontamination of fungal or high-nature organisms, in particular, depends on the conditions of storage, the type of plant used, and environmental factors [88].

5. Physiological and Biochemical Changes in Seeds After NTP Treatment

The stress induced on the plant can be evaluated from biochemical analyses of the seeds or the seedlings. Modifications detected at the biochemical level may include changes in the hormonal balance, activation of enzymes involved in the mobilisation of nutrient reserves in the endosperm, or even structural changes in the DNA that can influence gene expression [63]. It is also important to consider the long-term impact of the changes induced by cold plasma treatment, since there are indications that it could contribute to increasing the resistance of the plants to abiotic stress factors such as drought or extreme temperature variations, by stimulating intrinsic antioxidant mechanisms [31,33,42,76].

5.1. Stimulation of Germination

Non-thermal plasma treatment has emerged as a promising strategy to promote seed germination and stimulate early growth in leguminous plants. Research demonstrates that NTP enhances water uptake by increasing the wettability of the seed coat, thereby accelerating imbibition and facilitating the release of dormancy, particularly in hard-coated species such as alfalfa, fenugreek, and *Mimosa* [2,57,89–91]. Short exposure times (ranging from seconds to a few minutes) have been shown to optimise germination rates and seedling vigour in crops like soybean, mung bean, and pea, whereas prolonged treatment may exert inhibitory effects. On a physiological level, NTP stimulates seed metabolism by enhancing enzymatic activity (e.g., superoxide dismutase, catalase) and modulating phytohormone balance, which supports faster germination and more vigorous seedling development [41,92]. Field experiments further validate these findings, document-

ing yield improvements of up to 27% in blue lupine and 10% in peanut, primarily due to enhanced germination and improved resistance to pathogens [61]. In the study conducted by Li et al. in 2021, *Eremochloa ophiuroides* (centipedegrass) seeds were exposed to cold plasma across various power levels. A 120 W treatment produced the most significant enhancement: it notably increased germination rate, accelerated germination speed, and improved uniformity of emergence compared to untreated controls. These benefits were attributed to increased water uptake—evidenced by higher conductivity and lower contact angle—and more effective use of seed reserves, as seen by raised α -amylase and protease activities plus elevated sugar and protein levels [91]. The stimulation of seed germination by non-thermal plasma (NTP) arises from synergistic physical and biochemical mechanisms. Oxidation of the seed coat reduces the water contact angle and increases hydrophilicity, thereby facilitating imbibition and breaking dormancy, particularly in hard-coated seeds such as alfalfa and lupine. Microscopic analyses have confirmed surface alterations, including erosion of the cuticle and increased roughness, which enhance permeability to water and gases. At the same time, the antimicrobial action of reactive oxygen and nitrogen species (ROS/RNS) generated by plasma, such as ozone, hydrogen peroxide, and nitric oxide, effectively reduces microbial load on the seed surface, lowering the incidence of seedborne pathogens and ensuring healthier germination. Biochemical responses are also evident: hydrolytic enzymes such as α -amylase and dehydrogenase show increased activity, supporting nutrient mobilisation from seed reserves, while hormonal modulation is observed through decreased abscisic acid levels and elevated gibberellin concentrations, both favouring the release of dormancy [5,38,61]. Moreover, the mild oxidative stress induced by plasma enhances antioxidant capacity, as reflected in increased activities of superoxide dismutase and catalase, which strengthen the defence against abiotic stress [38,61]. Complementarily, plasma-activated water (PAW), enriched in nitrates and ROS, further contributes to improved nutrient uptake and activation of growth-related signalling, ultimately leading to stronger seedling development. Collectively, these findings indicate that NTP and PAW act synergistically to enhance germination, vigour, and stress resilience in leguminous seeds [48].

5.2. Increase in Antioxidant Levels

Seed treatment with non-thermal plasma (NTP) has been shown to exert a significant impact on antioxidant levels and oxidative stress in plants, influencing both germination and subsequent growth. Recent studies have demonstrated that seed exposure to NTP triggers a series of biochemical and physiological changes, including the generation of reactive oxygen and nitrogen species (RONS), which act as stress signals and activate plant defence mechanisms. These RONS, such as hydrogen peroxide (H_2O_2) and nitric oxide (NO), play a key role in regulating germination and in stimulating antioxidant systems. For instance, wheat, maize, and radish seeds treated with NTP exhibited increased levels of H_2O_2 along with enhanced activities of antioxidant enzymes, including superoxide dismutase (SOD), catalase (CAT), and peroxidase (POD), which neutralise free radicals and mitigate oxidative stress [56].

The mechanism by which NTP influences antioxidant levels involves both direct and indirect effects. On the one hand, reactive particles generated by plasma can directly interact with seed components, leading to oxidation of proteins, lipids, and other molecules, thereby activating plant defence responses. On the other hand, NTP can induce epigenetic modifications and gene expression changes, resulting in increased production of antioxidant enzymes and phenolic compounds with protective functions. For example, in rice seeds exposed to plasma, increased DNA methylation was detected in genes associated with

abscisic acid (ABA) metabolism, leading to improved germination and enhanced tolerance to heat stress [93].

In addition, plasma treatment can alter the composition of the seed-associated microbiome, indirectly affecting oxidative stress regulation. Some studies report that NTP reduces the presence of pathogenic microorganisms on the seed surface while promoting beneficial bacteria, which may alleviate oxidative stress through the production of bioactive compounds. Plants grown from plasma-treated seeds have also been found to accumulate higher levels of photosynthetic pigments and phenolic compounds, both of which contribute to protection against oxidative stress and to improved adaptability under adverse conditions [94]. These changes not only strengthen plant stress tolerance but also contribute to enhanced long-term productivity.

5.3. NTP Treatment of Seeds and Growth Hormones

Seed treatment with non-thermal plasma (NTP) has been shown to significantly influence phytohormone levels, with major implications for germination and subsequent plant development. Studies have demonstrated that NTP alters hormonal balance, particularly by increasing the ratio of gibberellic acid (GA) to abscisic acid (ABA), a key factor in dormancy release and germination stimulation [28,95]. The increase in the GA/ABA ratio favours the initiation of the germination processes specific to the second phase of imbibition, facilitating the transcription and translation of genes involved in the synthesis of hydrolytic enzymes. Plasma-generated reactive species have a dual role in this hormonal adjustment. ROS such as H_2O_2 act as second messengers that modulate gene expression of enzymes in the GA biosynthetic pathway, while RNS such as NO can directly interact with proteins from hormonal transduction systems [84]. For instance, plasma treatment of radish seeds resulted in decreased abscisic acid levels and elevated gibberellins concentrations, thereby facilitating germination. These effects vary depending on plant species, the physiological state of the seeds, and plasma treatment parameters [96]. Moderate oxidative signals resulting from exposure to NTP trigger the above-mentioned defence pathways, inducing a state of readiness for possible subsequent abiotic stressors.

In addition to gibberellins and abscisic acid, NTP can stimulate the production of other phytohormones such as auxins and cytokinin, having a strong impact on early cell division and differentiation of young tissue, and promote root and shoot growth [97]. Some studies have also reported elevated levels of jasmonates and salicylic acid, suggesting that plasma may activate plant defence mechanisms against stress. Epigenetic modifications, including DNA methylation, are thought to play a role in regulating the expression of hormone-related genes. Furthermore, NTP influences the signalling of reactive oxygen and nitrogen species (RONS), which interact with hormonal networks to fine-tune stress responses [98]. These effects may persist in the long term, shaping not only germination but also overall plant productivity through the modulation of phytohormone dynamics.

5.4. Activation of Enzymatic Metabolism

Seed treatment with non-thermal plasma (NTP) activates enzymatic metabolism through multiple mechanisms, inducing significant biochemical and physiological changes. Studies have demonstrated that seed exposure to NTP enhances the activity of enzymes involved in germination and growth, such as amylase, phytase, and protease, thereby facilitating the mobilisation of nutrient reserves from the endosperm or cotyledons [99]. High levels of these enzymes have been reported not only for model crops but also in agronomically important species such as beetroot or wheat, where there is a linear correlation between the enzymatic activity and final germination percentage [17,38,100]. Stimulation

of endogenous proteases that release amino acids necessary for the accelerated synthesis of structural and enzymatic proteins has also been observed.

Plasma treatment also reduces trypsin inhibition and phytic acid content, improving nutrient bioavailability. In addition, NTP promotes the generation of reactive oxygen and nitrogen species (RONS), which act as signalling molecules and trigger the activation of antioxidant enzymes such as superoxide dismutase, catalase, and peroxidase. These enzymes play a crucial role in mitigating oxidative stress and protecting plant cells against free radical damage, being essential for initiating and stimulating germination [44].

Beyond antioxidant enzymes, NTP influences secondary metabolism by stimulating the production of phenolic compounds, flavonoids, and other metabolites associated with plant defence. For instance, an increase in phenylalanine ammonia-lyase (PAL) activity, a key enzyme in phenyl propanoid biosynthesis of phenolic compounds with antioxidant and antimicrobial roles, has been reported. This change indicates the integration of NTP effects into a complex, systematic response which includes secondary metabolites as protective elements in the early ontogenetic stages of the plants. NTP treatment also regulates the enzyme guaiacol peroxidase (G-POX), relevant for the controlled oxidation of phenolic compounds and modulation of cell turgor through fine oxidative remodelling of the cell walls [1]. All enzymatic effects must be viewed from the perspective of synchronisation: plasma treatment rebalance in initial variability and activity of hydrolytic or antioxidant enzymes between different seeds in the batch so that the mobilisation of nutrients and defence system occurs in a more compressed time interval, which leads to a more uniform germination. Analyses comparing several species confirm that these processes of enzyme stimulation and increased activity of the antioxidant systems are an essential biochemical core for the germination and early growth of the plants following NTP treatment of the seeds. Balancing these factors can be performed by tuning plasma components to maximise the agronomic benefits without compromising the biological integrity of the seeds [43].

5.5. Impact on DNA: Damage or Adaptations

The impact of non-thermal plasma on seed DNA is a complex subject that covers both potential genetic damage and adaptive responses that may enhance plant stress tolerance. Recent studies indicate that exposure to non-thermal plasma can induce alterations in deoxyribonucleic acid structure while simultaneously activating repair and adaptation mechanisms. Reactive oxygen species and reactive nitrogen species, together with ultraviolet and vacuum ultraviolet radiation generated during plasma treatment, are capable of interacting with embryonic deoxyribonucleic acid [63]. Experimental evidence has shown that plasma may cause double-strand breaks and fragmentation in isolated deoxyribonucleic acid; however, within intact seeds, the protective role of the seed coat and cell walls mitigates the extent of such damage. For example, pea seeds treated with non-thermal plasma did not exhibit significant DNA damage but instead displayed enhanced repair mechanisms that reduced the detrimental effects of toxic agents such as zeocin [101]. Beyond direct genotoxic effects, non-thermal plasma has been shown to influence epigenetic regulation. In *Arabidopsis thaliana*, plasma exposure increased deoxyribonucleic acid methylation, altering the expression of genes associated with growth and stress responses. A decrease in the expression of transcriptional repressors, combined with the upregulation of genes involved in methylation, suggested an adaptive epigenetic response [102]. Conversely, soybean seeds exhibited reduced DNA methylation following plasma treatment, which correlated with enhanced expression of genes related to energy metabolism and growth. These findings highlight the species-specific nature of plasma-induced epigenetic modifications [103]. At the transcriptional and metabolic level, non-thermal plasma has been reported to regulate genes associated with photosynthesis, carbon fixation, and

phytohormone synthesis, particularly auxin [102]. Concurrently, increased activities of antioxidant enzymes, including superoxide dismutase, catalase, and peroxidase, were observed, contributing to enhanced protection against oxidative stress [5]. While these findings provide valuable insights into the genetic and epigenetic effects of plasma on seeds, further studies are necessary to elucidate the underlying molecular mechanisms fully and to optimise plasma applications in seed technology. Plasma treatment can also induce changes in DNA methylation and alter the expression of genes related to energy metabolism, including ATP synthase subunits, thereby contributing to faster germination and enhanced plant growth [104].

6. Challenges and Future Directions

Assessing the safety of NTP agricultural applications is essential for validating this technology and gaining acceptance from the farmers and regulatory authorities. Despite having so many advantages—the absence of toxic residues, energy savings, the germination and growth promotion—large-scale implementation requires a rigorous analysis of the potential adverse effects on the treated products, environment, and human or animal health. There is a need for systematic studies, over extended periods, covering a wide variety of crops. The central safety element is the management of reactive species, which are indispensable for the stimulatory effects, but at uncontrolled doses, they can harm the operator or consumer, as in the case of ozone or nitrogen oxides. Monitoring these species in the active treatment zone in ambient air should become an integral part of work protocols, while the design of NTP generators must minimise uncontrolled dispersion into adjacent spaces. UV radiation produced locally can also present a risk for the operator.

Major challenges remain related to the transfer of the technology from the lab to the farm. Among these, the most important is defining standardised protocols depending on the agricultural species, assessing long-term effects on the crops and agricultural ecosystems, as well as the economic viability for integrating the technology into current production chains. Optimised processing conditions will contribute to both the scalability of the method and to maximising its benefits in the context of global food security.

The application of NTP treatments in the seed industry for germination improvement can present several significant limitations [19]:

- Lack of parameter standardisation—a wide variety of plasma devices and configurations (DBD, plasma jet, corona discharge, etc.), each with specific parameters (voltage, frequency, exposure time, working gas). This makes it difficult to compare results and the reproducibility of treatments.
- Irreproducible effects—due to the complexity of the interaction between plasma and the seed surface, the results can vary significantly depending on the plant species, variety, initial seed condition, and environmental conditions.
- Lack of understanding of molecular mechanisms—although it is known that reactive oxygen and nitrogen species (ROS/RNS) play a key role, the exact mechanisms by which plasma influences gene expression, hormonal signalling, and secondary metabolism remain unclear.
- Potential risk of phytotoxicity—prolonged treatments or those with non-optimised parameters can induce excessive oxidative stress, affecting seed viability and plant development.
- Industrial scalability—large-scale application is still a challenge due to equipment costs, the need for real-time monitoring, and the lack of standardised protocols for different crops.
- Lack of long-term studies—the effects of plasma treatment on future generations of plants and on the ecosystem are not sufficiently studied.

Therefore, successfully integrating NTP treatments into agricultural practices requires an interdisciplinary framework, thus the need for collaboration between various scientific and technical fields to optimise each element in the operational chain. It is very important to correlate plasma parameters with the biological responses of the seeds to understand, optimise, and control the mechanisms of interactions. Such a framework would also allow the identification of critical thresholds from the perspective of the synergistic impact of plasma components on plant performance.

Another important direction is combining plasma treatments with other established methods for seed stimulation or protection, as some researchers have performed. In this way, hybrid protocols can be developed, combining plasma treatment with the use of bacterial cultures, nanomaterials, or different substances.

Adjusting the NTP treatments to seed species is another critical aspect that must be considered to maximise the technological efficiency and prevent adverse effects. The structural and physiological diversity of seeds requires a fine adjustment of the operational parameters. Some seeds have a thick and lignin-rich structure (e.g., maize, sunflower), which is a barrier harder to penetrate, needing longer treatments and higher power [13,66]. In contrast, seeds with a thin seed coat (e.g., lettuce, tomato) react quickly to moderate treatments, risking oxidative degradation [44].

7. Conclusions

Cold plasma technology is an innovative and promising biotechnological method, with significant potential to improve seed and crop performance through a low-temperature treatment that preserves the biological integrity of the plant material. The complex interactions between plasma components and the structure of the seed coat leads to morphological, chemical and physiological changes that accelerate germination and support the development of the seedlings. It is essential to adjust treatment parameters such as discharge power, exposure time, and feed gas to maximise the beneficial effects and reduce oxidative or mechanical damage.

Different NTP configurations, from low pressure ones to atmospheric pressure and hybrid systems, offer flexibility in application, allowing the treatment of both large batches and individual seeds with increased uniformity. The induced modifications in the seed surface morphology, such as increased porosity, microcracks, and chemical functionalisation, lead mostly to a decrease in the contact angle and facilitate the water uptake and initiation of germination. At the biochemical level, NTP treatments stimulate the activity of enzymes involved in the mobilisation of the nutrient reserves, regulate the hormonal balance, and activate antioxidant systems, preparing the seeds for abiotic stress conditions. There is also evidence of epigenetic adaptations that can influence gene expression, contributing to the resilience of the resulting seedling.

Major challenges are faced in correlating plasma parameters to the biological outcomes, revealing the mechanisms of interaction, and controlling it. Another challenge is related to scaling up the devices and bringing NTP from the lab to the field. Overall, NTP is emerging as a modern, versatile, and environmentally friendly technology that is able to significantly contribute to increasing productivity and protecting the environment, thereby responding to the current challenges of global food security.

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Abbreviations

The following abbreviations are used in this manuscript:

NTP	Non-thermal plasma
SEM	Scanning electron microscopy
DBD	Dielectric barrier discharge
UV	Ultraviolet
DNA	Deoxyribonucleic acid
RF	radiofrequency
FEDBD	Floating electrode dielectric barrier discharge
HV	High voltage
DCSBD	Diffuse coplanar surface barrier discharge
LPRF	Low pressure radiofrequency
FTIR	Fourier transform infrared
XPS	X-ray photoelectron spectroscopy
LPDBD	Low pressure dielectric barrier discharge
SCP	Streamer corona plasma
RONs	Reactive oxygen and nitrogen species
ROS	Reactive oxygen species
RNS	Reactive nitrogen species
APPJ	Atmospheric pressure plasma jet
EDS	Energy-dispersive X-ray spectroscopy
WCA	Water contact angle
ATP	Adenosine triphosphate
NO	Nitric oxide
SOD	Superoxide dismutase
CAT	Catalase
POD	peroxidase
GA	Gibberellic acid
ABA	Absciscic acid
PAL	Phenylalanine ammonia-lyase
G-POX	Guaiacol peroxidase

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