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Review

The Effects of Plasma on Plant Growth, Development, and Sustainability

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Abstract: Cold atmospheric or low pressure plasma has activation effects on seed germination, plant growth and development, and plant sustainability, and prior experimental studies showing these effects are summarized in this review. The accumulated data indicate that the reactive species generated by cold plasma at atmospheric or low pressure may be involved in changing and activating the physical and chemical properties, physiology, and biochemical and molecular processes in plants, which enhances germination, growth, and sustainability. Although laboratory and field experiments are still required, plasma may represent a tool for efficient adaptation to changes in the climate and agricultural environments.

Keywords: plasma; seed germination; plant growth; plant sustainability; stress tolerance; reactive species

1. Introduction

Agriculture faces many problems due to continuous global population growth, environmental pollution, lack of agricultural land, and climate change. Climate change, in particular, has caused significant reductions in crop yield, threatening global food security [1]. According to the Food and Agriculture Organization (FAO), 20–45%, 5–50%, and 20–30% yield reductions are expected for maize, wheat, and rice, respectively, by 2100 under the current rates of climate change [1]. The distribution of plant pathogens and pests has shifted, the virulence of pathogens has been altered, and new diseases have emerged as a consequence of climatic changes [2,3]. Climate change has also altered the optimal locations of crop culture and reduced the quality and quantity of crop products [4].

Various strategies and technologies have been developed to adapt to changing agricultural environments. Efficient land use and management, altered food demand patterns, and reduced food waste and loss are often suggested as adaptation strategies [5]. Technological crop improvements also provide reliable solutions to overcome environment-associated challenges. Genetic engineering and breeding-based technologies are frequently used to produce crop plants with higher yield and stress tolerance [5]. However, the genetic regulations for crop production and tolerance are complicated processes involving many genes, which complicates crop improvement via genetic manipulation. Safety issues are another barrier that limits the broad application of genetic approaches.

The multi-disciplinary approach has received great attention, and cold atmospheric or low pressure plasma developed by physicists has been actively explored for its agricultural applications [6]. Plasma is an ionized gas produced at room temperature under atmospheric pressure. It generates reactive species, so the activation of plant vitality and the inactivation of microorganisms are frequently observed in agricultural applications [6]. Cold atmospheric or low pressure plasma is a potential tool to increase crop plant vitality and production, and several studies have investigated plasma-induced improvements to seed germination, plant growth and reproduction, and plant sustainability. In this review, we summarize the agriculture-based studies of cold atmospheric or low pressure plasma. Due to space limitations, we are unable to review all the published work in this rapidly expanding field.

2. Effect of Plasma on Seed Germination

Seeds are the reproductive products of plants which have totipotency, i.e., the capacity to develop into whole plants. Seeds are necessary for plant survival, dispersal, and the maintenance of progeny. At the time of dispersal, seeds undergo a period of dormancy to avoid unfavorable environmental conditions. Many dormant seeds fail to germinate, even if favorable conditions exist. Therefore, it is necessary to break the dormancy stage to increase germination. Other than the environmental factors, the dormant phase and seed germination are influenced by the hard seed coat, the presence of inhibitors, the seed maturation period, the immature embryo, seed coat impermeability to oxygen and water, and hormone imbalances. The phytohormone abscisic acid (ABA) is responsible for maintaining dormancy, whereas gibberellic acid (GA) is responsible for breaking the dormancy phase. These phytohormones are synthesized in the seeds in response to physical factors, and they activate the signaling cascades and enzymes that promote the degradation of seed reserves and initiate germination. Germination occurs in different phases and involves various physiological, biochemical, and molecular events (Figure 1).

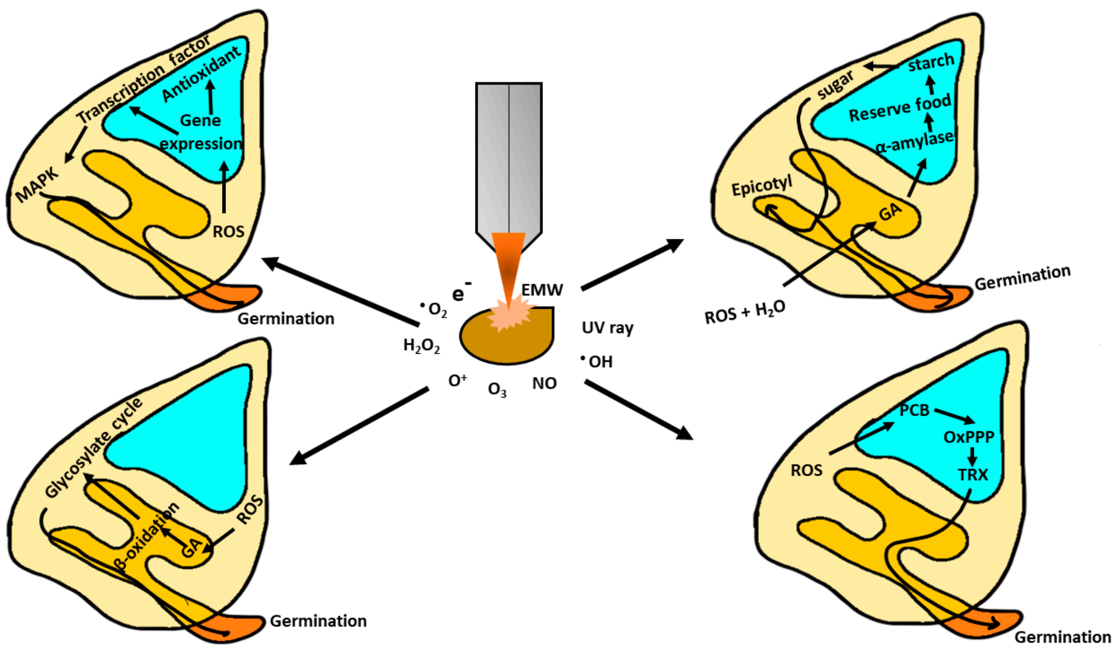

Figure 1. Plausible events of seed germination initiated by plasma seed priming. Plasma treatment causes mechanical damage and facilitates a redox environment for the seed. This redox environment induces different pathways of seed germination. EMW: Electromagnetic wave, GA: Gibberellic acid, MAPK: Mitogen activated protein kinase, OxPPP: Oxidative pentose phosphate pathway, PCB: Protein carbonylation, TRX: Thioredoxin.

Various seed treatment procedures have been applied to overcome dormancy. Popular seed treatment or priming methods, such as scarification, stratification, and chemical treatments, are used to induce germination in dormant seeds [7]. Cold (non-thermal) atmospheric or low pressure plasma is a new technology to enhance seed germination (Tables 1 and 2), and seed treatment involves (1) direct exposure to plasma (Table 1) or (2) indirect exposure via plasma-treated water and solutions (Table 2).

Table 1. Effects of direct plasma on plant germination, growth, and physiology.

Plant Species	Plasma Source	Feeder Gas	Treated Stage	Enhanced Effects	Reference
Avena sativa *Hordeum vulgare*	Glow discharge air plasma	Air	Seed	Germination	[8]
Hordeum vulgare *Raphanus sativus* *Pisum sativum* *Glycine max* L. Merr. *Zea mays* L. *Phaseolus vulgaris* L.	Low-pressure RF (radio frequency) rotating plasma	carbon tetrafluoride (CF4)/octadecafluorodeca-lin (ODFD)	Seed	Germination	[9]
Lycopersicon esculentum L. Mill. cv. Zhongshu No. 6	Magnetized plasma		Seedling	Growth and productivity	[10]
Chenopodium album agg.	Low-pressure microwave plasma	Mixture of Argon (Ar), Nitrogen (N_2), and Oxygen (O_2)	Seed	Germination	[11,12]
Avena sativa *Triticum aestivum*	Plasma plant Plasonic AR-550-M	Air	Seed	Germination and early growth	[13]
Lupinus angustifolius Galega virginiana Melilotus albus	RF air Plasma	Air	Seed	Germination and productivity	[14]
Solanum lycopersicum	DBD (dielectric barrier discharge) air plasma	Air	Seed	Growth and yield	[15]
Lens culinaris *Phaseolus vulgaris* *Triticum*	Cold radiofrequency Air plasma	Air	Seed	Germination	[16]
Fagopyrum aeseulentum	GlidArc plasma Surface DBD plasma Downstream microwave plasma Planar rotating electrode plasma	Air and mixture of air with water vapors	Seed	Germination (depending on plasma sources)	[17]
Glycine max L. Merr. cv. Zhongdou 40	Low-pressure RF helium plasma	Vacuum	Seed and seedling	Germination and growth	[18]
Raphanus sativum var. Icicle	Surface discharge plasma	Air	Seed	Early growth	[19]
Andrographis paniculata	DBD air plasma	Air	Seed	Germination and growth	[20]
Pisum sativum	Surface DBD plasma	Air	Seed, sprout, and seedling	Germination and flavonol glycoside	[21]
Triticum aestivum	Surface discharge plasma	Air	Seed and vegetative stage	Germination and growth	[22]
Raphanus sativus var. *longipinnatus*	DBD plasma	Pure Oxygen (O_2)	Seed and vegetative stage	Germination and growth	[23]
Coriander sativum	DBD N_2 (nitrogen) plasma Microwave plasma generated gas	Nitrogen (N_2)	Seed	Germination	[24]
Brassicaceae	Low-pressure RF O_2 (oxygen) plasma	Oxygen (O_2)	Seed	Antioxidant activity	[25]
Arabidopsis thaliana	Gliding arc air plasma	Air	Seed and reproductive stage	Germination and growth	[26]
Pisum sativum L. var. Prophet	Diffuse coplanar surface DBD plasma	Air	Seed and seedling	Germination and growth	[27]

Table 1. *Cont.*

Plant Species	Plasma Source	Feeder Gas	Treated Stage	Enhanced Effects	Reference
Spinacia oleracea L.	High voltage nanosecond pulsed plasma Micro DBD plasma	Air and nitrogen (N_2) gas	Seed	Germination and growth	[28]
Erythrina velutina	DBD He plasma	Helium (He) gas	Seed	Germination	[29]
Hordeum vulgare	Surface DBD plasma	Nitrogen (N_2) with bubble air	Seed	Germination, growth, and GABA content	[30]
Raphanus sativus L.	DBD plasma with various feeding gases	Air, oxygen (O_2), nitrogen (N_2), helium(He), argon (Ar), and NO(10%)+nitrogen	Seed	Growth (depending on feeding gas and moisture)	[31]
Mung bean	DBD plasma generated in water using various gas	Air, oxygen (O_2), nitrogen (N_2), and helium (He)	Seed	Germination and growth	[32]
Brassica juncea L.	Nanosecond microspark plasma	Air	Seed	Germination	[33]
Chenopodium quinoa	DBD RF air plasma under atmospheric and low pressure	Air	Seed	Germination	[34]
Wheat	DBD plasma with various feeding gases	Air, oxygen (O_2), nitrogen (N_2), and argon (Ar)	Seed	Germination and growth	[35]
Lavatera thuringiaca L.	Gliding arc discharge N_2 plasma	Nitrogen (N_2)	Seed	Germination	[36]
Capsicum annuum	DBD Ar (argon) plasma	Argon (Ar)	Seed	Growth	[37]
Cannabis sativa L.	Gliding arc plasma Microwave plasma	Oxygen (O_2) and argon (Ar)	Seed and vegetative stage	Germination and growth	[38]
Mimosa caesalpiniafolia	DBD plasma	Air	Seed	Germination	[39]
Glycine max L. Merrill	DBD Ar plasma	Argon (Ar)	Seed	Germination and growth	[40]
Sunflower	Ar/O_2 plasma	Oxygen (O_2) and argon (Ar)	Seed	Growth	[41]
Lavatera thuringiaca L.	DBD plasma jet with N_2/He gas	Nitrogen (N_2), and helium (He)	Seed	Germination	[42]
Wheat	Low-pressure DBD plasma with Ar/O_2 and Ar/air gases	Air, oxygen (O_2) and argon (Ar)	Seed	Germination and growth	[43]
Corn	Microwave plasma jet DBD He plasma Low-pressure RF N_2 plasma	Nitrogen (N_2), and helium (He)	Seed	Growth and yield (field)	[44]
Trigonella foenum-graecum	Ar plasma jet	Argon (Ar)	Seed	Germination and growth	[45]
Allium sativum Ptujski spomladanski	Low-pressure RF O_2 plasma	Oxygen (O_2)	Seed and seedling	Germination and growth	[46]
Triticum spp.	Ar plasma Q-switched Nd:YAG (Quantel Brilliant) pulsed laser	Argon (Ar)	Seed	Germination and sterilization	[47]
Zoysia willd.	Low-vaccum He plasma	Helium (He) and air	Seedling	Growth	[48]

Table 1. *Cont.*

Plant Species	Plasma Source	Feeder Gas	Treated Stage	Enhanced Effects	Reference
Glycine max L. Merrill	DBD plasma	Oxygen (O_2) and nitrogen (N_2)	Seed and seedling	Germination and growth	[49]
Cucurbita pepo L. cv. Cinderella *Cucurbita maxima* L. cv. Jarrahdale *Cucurbita maxima* L. cv. Warty Goblin	Cold atmospheric pressure plasma	Helium (He) and argon (Ar)	Seed	Germination	[50]
Cichorium intybus	DBD plasma (Model PS200)	Argon (Ar)	Seed and seedling	Germination, growth, and flowering	[51]
Ocimum basilicum	Volume barrier discharge plasma	Humid Air (40% RH)	Seed	Germination	[52]
Catharanthus roseus	DBD plasma	Argon (Ar)	Seed	Growth and physiology	[53]
Vitis vinifera	DBD Ar plasma	Argon (Ar)	Seed and seedling	Germination and growth	[54]

Table 2. Effects of plasma treated water/solution on plant germination, growth, and physiology.

Plant Species	Plasma Source	Feeder Gas	Treated Stage	Enhanced Effects	Reference
Citrullus lanatus *Zinnia peruviana* *Medicago sativa* *Phaseolus cocconeus*	Plasma-treated water	Air	Vegetative stage	Growth	[55]
Janie marigold Better Boy tomato Early Scarlet radish	Plasma-treated water	Air	Seed and seedling	Growth	[56]
Raphanus sativus *Solanum lycopersicum* *Capsicum annum*	DBD air plasma and Plasma activated water	Air	Seed and vegetative stage	Germination and growth	[57]
Arabidopsis thaliana	DBD air and He (helium) plasma Plasma-treated water	Air and Helium (He)	Seed and seedling	Germination and growth	[58]
Coral lentils (*Lens culinaris*)	Plasma-treated tap water	Air	Seed	Growth	[59]
Glycine max L. Merrill	Plasma-treated water	Air	Seed	Growth and quality	[60]
Solanum lycopersicum	Plasma-treated water	Air	Seedling	Growth	[61]
Pisum sativum L.	DBD plasma Plasma-treated tap water	Air	Seed and seedling	Germination, growth, and flowering	[62]
Radish sprout	Plasma-treated organic solutions	Argon (Ar) and oxygen (O_2) mixture	Seedling	Growth	[63]
Spinacia oleracea L.	Plasma-treated water	Mixture of oxygen (O_2) and nitrogen (N_2)	Seed	Growth	[64]
Tomato Lettuce Mung bean Sticky bean Radish Dianthus Mustard Wheat	DBD plasma Plasma-treated water	Air, oxygen (O_2) and nitrogen (N_2)	Seed	Germination and growth	[65]
Mung bean	Plasma-treated water	Air, oxygen (O_2), nitrogen (N_2), and helium (He)	Seed	Germination and disease tolerance	[66]

The first reported case of plasma application to seeds was in a US patent by Krapivina et al. [67], where cold atmospheric pressure plasma generated from a mixture of inorganic gases (atmospheric air, oxygen, and nitrogen) was applied to soybean seeds for 5 to 300 s and the germination and growth were enhanced [67]. In the past 20 years, various plasma sources (dielectric barrier discharge (DBD) jet plasma, microwave discharge, radio-frequency (RF) discharge, gliding discharge) have been developed and used for treating vegetables (tomato, radish, coriander, green peas, and sunflower) and crops (rapeseed, cotton, maize, oat, wheat, mustard, soybean, legumes, and honey clover) (Table 1). Plasma treatment (direct or indirect) has enhanced seed germination in most studies, although no changes in the germination percentage were observed in several studies [15,19,41,44,56,59,64]. Plasma promoted the germination speed, overall germination percentage, or both.

Studies have also demonstrated variable effects on seed germination depending on the plasma sources, plant species, treatment time, feeding gases, and moisture content. Šerá et al. [17] compared different plasma sources for buckwheat seed germination and found that a GlidArc plasma source with an air feeder gas induced improved germination compared to downstream microwave plasma, planar rotating electrode plasma, and surface dielectric barrier discharge plasma. Other studies have reported variations in seed germination efficiency among plant species when treated with the same plasma source (Tables 1 and 2) [9,13,14,16,46,50,56,57,65]. Most studies identified an optimal treatment time for the best germination efficiency for each plant species and plasma source. Effects of the feeding gases on the plasma-mediated seed germination have also been reported. Zhou et al. [32] found that mung bean seed germination was most efficient with microplasma generated in an aqueous solution using oxygen as the feeding gas, as opposed to helium, nitrogen, and air. Meng et al. [35] reported germination increases of 24, 28, and 35.5% for DBD plasma-treated wheat seeds with air, nitrogen, and argon feeding gases, respectively. Most studies have been under laboratory conditions, but field-based investigations have also been reported [14,44]. Filatova et al. [14] observed a 10–20% increase in the field germination capacity of soy, honey clover, and catgut seeds with microwave plasma treatment, whereas Ahn et al. [44] did not observe any changes in the germination percentage.

The mechanisms of enhanced seed germination by plasma have been thoroughly investigated. The most frequently reported factors are changes in the physical and chemical properties of the seed coat or surface. Physical and chemical changes to the seed surface can result in elevated hydrophilicity and water permeability that enhances water imbibition, which is required for seed germination. Increased hydrophilicity and water permeability of the seed surface after plasma treatment has been frequently observed [16,68,69]. Chemical changes and leaching of the seed surface membrane have also been analyzed in many studies [14,18,34,42,68]. Cold atmospheric pressure plasma decreases the water contact angle from 115° to 0° and modulates the hydrophilicity of the seed surface, which increases the uptake of water and initiates subsequent biochemical processes [16]. Similarly, Ling et al. [18] reported that cold plasma treatment decreases the contact angle of soybean seeds from 70.14° to 20.94°. There is abundant data to support the plasma-induced changes in the physicochemical properties of the seed surface and the increases in water absorption. However, enhanced seed germination was also observed without increased hydrophilicity of the seed surface [34]. The surface of quinoa seeds treated with RF plasma was chemically modified, but the hydrophilicity of the seed surface did not change. Nitrogen oxide (NO_x^-) and potassium (K^+) ions accumulated on the seed surface via chemical alterations from the plasma treatment and penetrated the seeds after water addition, providing nutrients for seed germination. Another possible mechanism for plasma-induced enhanced seed germination is that the biochemical and molecular processes inside the seed are activated by plasma generated reactive oxygen and nitrogen species (RONS). Plasma generates a diverse range of RONS, depending on the feeder gas. These RONS can act as signaling molecules and initiate a germination cascade [70]. Reactive oxygen species (ROS) facilitate the oxidation of the aleurone layer and the mobilization food reserves during seed germination. Mildažienė et al. [71] showed that RF cold plasma (at low pressure) treatment (7 min) increased the GA (gibberellic acid) content of sunflower seeds and increased the germination rate by 10–24%. Increased GA promotes the activity of α-amylase, which degrades complex starches to metabolize sugar to initiate the germination process [71]. Accumulation of the GA_3 germination hormone and amylolytic mRNA in spinach seeds treated with DBD plasma has also been reported [28]. Rahman et al. [43] detected high concentrations of hydrogen peroxide (H_2O_2) in cold plasma (Ar/Air, at low pressure) treated seeds and concluded that H_2O_2 is a signaling molecule that stimulates seed germination. Hydrogen peroxide serves to maintain a low ABA/GA ratio, which promotes the activation of amylase, the mobilization of food reserves, and the low production of antioxidant enzymes. Nitric oxide (NO) is another reactive species that plays a regulatory role in seed germination. NO regulates the production of ABA, a vital phytohormone that initiates germination and breaks dormancy. In plants, NO is produced from the reduction of nitrate (NO_3^-) to nitrite (NO_2^-) by nitrate reductase. Hence, NO_3^- in plasma-activated water is primarily responsible for enhanced seed germination [57]. A model of the plasma effects on seed germination and the possible molecular and biochemical events is presented in Figure 1.

3. Effects of Plasma on Plant Vegetative Growth and Reproduction

The life cycle of plants is divided into three distinct phases: vegetative, reproductive, and seed formation, followed by senescence. Vegetative growth is an important phase in which plants perform photosynthesis, increase their biomass, synthesize the reserve food, and prepare for reproduction. It is also a very sensitive stage because growth is influenced by environmental factors (i.e., heat, drought, pathogen, alkalinity, UV rays) and biological stimuli. Overall crop productivity depends on the vegetative growth phase, and, therefore, the regulation of vegetative growth is critical for plant development and survival [72].

Plasma can regulate the vegetative growth phase of plants, and plasma seed treatment has long-term effects on the early vegetative growth, as reported in several studies (Table 1). Plasma treatment promotes seed germination and subsequent seedling growth, increasing the length and biomass of seedlings (Table 1). As mentioned earlier, enhanced seedling growth without changes to the germination efficiency has been also observed after plasma treatment [15,19,41,44,56,59,64]. Plasma treatment at the seedling stage has also reported, which promoted seedling growth [10,48,55,61,63]. As for seed germination, the effects of plasma on seedling growth varies with the plasma dose, treatment time, feeding gases, and moisture. Extended plasma exposure or high power or atmospheric pressure reduced seedling growth; wheat seeds treated for 3 min had higher sprout biomass than seeds treated for 10, 20, or 40 min [13]. Milder plasma treatments (2.7 W) accelerates early growth and increases the root to shoot ratio [22]. Sarinont et al. [31] investigated the effects of feeding gases and moisture on plasma-mediated seedling growth and found that DBD plasma-treated radish seeds had better seedling growth when air, oxygen (O_2), nitric oxide (NO) (10%), and nitrogen (N_2) were used as the feeding gases (rather than N_2, helium (He), and argon (Ar)). Additional moisture during plasma treatment also accelerated the growth enhancement effects.

Compared to vegetative growth, the effects of plasma on flowering and fruit production have rarely been reported. Studies have shown that plasma seed treatment has positive effects on the reproductive stage and harvesting product of tomatoes, soybeans, and peanuts [10,49]. A field study of okra (*Abelmoschus esculentus*) in India, found that cold low pressure plasma seed treatment improved different agronomic attributes, including the harvesting time, 50% flowering time, flower number, fruit number and weight, and okra yield [73]. Recently, Li et al. [74] reported increase in pod numbers (13.8%) and grain weight (8.2%) after priming oilseed rape plants with cold low pressure plasma at the reproduction stage. In another report, cold atmospheric pressure plasma seed priming increased the flower number (41.5%) and fresh weight (24%) in *Cichorium intybus* [51]. Cold atmospheric pressure plasma treatment alone or as a co-treatment with multi-walled carbon nanotubes increased the flower number and diameter of melons, which resulted in more melon fruits [75].

When investigating the mechanism of plasma action on seedling growth, many reports have focused on the increased nitrogen nutrient levels, changes in the amount growth hormones and other physiological processes, and the activation of growth-related gene expression. These mechanisms are likely related to the plasma-generated reactive species. Plasma-generated reactive species can produce nitrogen species, such as NO_2^- and NO_3^-, after interacting with water. Plasma-treated water acts as a nitrogen fertilizer and is responsible for growth induction in seedlings [57]. Other reactive species, such as H_2O_2 and NO, can act as growth stimulators. These reactive species may disturb redox homeostasis and trigger mild oxidative stress in plants at the vegetative and reproductive stages. Elevated in situ H_2O_2 and NO_x concentrations in tomato seedlings in response to plasma-activated water (PAW) was detected by Adhikari et al. [61]. Similar observations the accumulation of RONS in response to plasma treatment in plants have also been reported in other studies [43,54]. The impact of RONS on plant development is well known [76,77], so plasma-generated RONS may similarly influence plant growth and development. Redox reactions play an important role in the cell cycle and cytokinesis. Many small antioxidants (i.e., ascorbate and glutathione) are essential for the cell cycle and act as redox buffers [78,79]. A study of wheat (*Triticum sp.*) and Arabidopsis roots suggests that the chemical impediment of ROS disturbs microtubule assembly and promotes microtubule formation in the root tip cells. This disturbance to tubulin organization leads to a distorted cytokinesis process [80]. ROS, such as H_2O_2, hydroxyl radical ($OH^\bullet$), and superoxide ($O_2^-\bullet$, affect cell expansion via their control of the cell wall rigidity. Peroxidase in the apoplasts maintains the H_2O_2 level, regulates the crosslinking of phenolics and extensins, and maintains the cell wall rigidity. In contrast, $OH^\bullet$ oxidizes polysaccharides (e.g., xyloglucans and pectins) and facilitates cell wall loosening [76]. Another study showed that the $O_2^-\bullet$ gradient in the meristem of the roots can play a role in cell division—high $O_2^-\bullet$ levels are present in root tips, the highest cell division zone, and the peripheral elongation zone has high H_2O_2 levels [81]. In *Arabidopsis*, the ROS content varies during floral bud formation and maturation, indicating the crucial role of ROS during flower development. In rice, the MADS3 gene, which is responsible for stamen formation during early floral bud development, regulates the $O_2^-\bullet$ concentration. Abnormal MADS3 expression causes pollen sterility by accumulating $O_2^-\bullet$ [82]. ROS can crosstalk with phytohormones and influence plant growth and development. In the roots, meristem cell growth is influenced by the interplay of H_2O_2 and brassinosteroids (BRs); intracellular H_2O_2 induces the binding of BR to its receptor kinase BRI. H_2O_2 can oxidize BZR1 (Brassinazole-Resistant 1) and BES1 (Brassinosteroid insensitive 1-Emssuppressor 1), the key transcription factors of BR signaling, and modify their activities. BZR1 interacts with PIF4 (Phytochrome Interacting Factor 4) and ARF6 (Auxin Response Factor 6), which are responsible for promoting meristem growth and development [83]. The redox reaction and ROS also regulate the post-translational modification of histones, transcription factors, and the chemical modifications of the nitrogenous DNA bases. Therefore, ROS epigenetically regulates plant growth. Under oxidative stress, ROS downregulates the histone demethylase gene, interacts with DME1 (DNA methylase), and epigenetically modifies the stress response of plants [77].

Seed reserve food utilization and the contents of soluble sugar and protein in seedlings are elevated after plasma treatments [84]. Cold atmospheric pressure plasma treatment of seeds affects the growth hormone concentration in the vegetative stage. Stolárik et al. [27] observed that the concentration of auxin (IAA) was upregulated in 14- and 21-day-old seedlings exposed to LTP (low-thermal plasma) for 120 s and 600 s at the seed stage. Interestingly, the cytokinin content was also significantly increased in 14 days old seedlings exposed to LTP for 120 s (compared to non-exposed seedlings) [27]. Other reports suggest that the redox homeostasis of plants is modified by cold atmospheric or low pressure plasma treatment. The modulation of superoxide dismutase (SOD), ascorbate peroxidase (APX), and chloramphenicol acetyltransferase (CAT) enzyme activities was observed in wheat plants after low pressure DBD plasma exposure [43]. Likewise, changes in the antioxidant (proline, ascorbic, guaiacol peroxidase, phenylalanine ammonia-lyase, phenolic, and flavonoid) status were also observed in plants at the vegetative stage after cold atmospheric pressure plasma treatment [40,61,85,86]. The expression patterns of different growth-regulating genes in response to cold atmospheric pressure plasma treatment have been investigated—argon plasma downregulates the expression of the methylation-related genes in soybeans and epigenetically regulates the expression of the metabolism-related genes [40].

The underlying mechanisms of RONS in plant growth and development are well known, and enormous amounts of information are available. As indicated by several studies, cold plasma and plasma-activated solutions can act as oxidative stimulants and disturb redox equilibrium. Redox non-equilibrium promotes the interaction of RONS with biomolecules, leading to oxidative modification or damage. Elevated RONS can also crosstalk with other metabolic reactions, phytohormones, and growth and development signaling cascades that change the plant across different physiological, biochemical, and molecular levels (Figure 2).

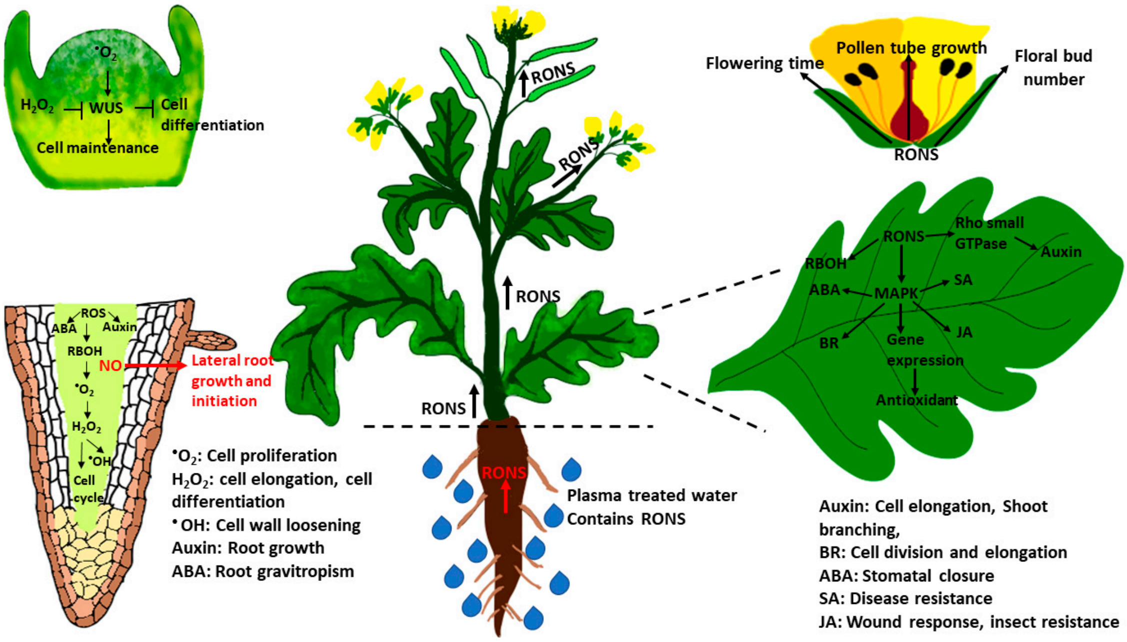

Figure 2. Effects of plasma-generated reactive oxygen and nitrogen species (RONS) in different plant organs at different growth stages. Direct and indirect exposure to plasma induces RONS in various plant organs (shoots, roots, leaves, and flowers) and activates different signaling cascades that crosstalk with other small signaling molecules and hormones to affect growth, development, and immunity. BR: Brassinosteroid, ABA: Abscisic acid, SA: Salicylic acid, JA: Jasmonic acid, MAPK: Mitogen activated protein kinase, WUS: WUSCHEL.

4. Plasma Technology for Crop Sustainability and Food Processing

Sustainable crop production and food security are important issues for modern society. Therefore, the development of technologies to address these issues is urgently needed. Sustainable agriculture technologies can not only increase crop production and tolerance but also help to preserve natural resources and ecosystems. Cold atmospheric or low pressure plasma is a modern-age technique that may alleviate the risks associated with agriculture and food processing systems. Cold atmospheric or low pressure plasma is an eco-friendly approach that positively affects crop production under adverse conditions. Various biotic and abiotic factors affect crop production, and several old agrochemical and biotechnological approaches have been used to address these issues. However, they often have negative impacts on the ecosystem. Plasma represents a risk-free approach because it requires low energy, is waste-free, and has no negative effects on the environment.

The effects of cold atmospheric or low pressure plasma treatment on seed germination and seedling growth under drought, salt, and chemical toxicity have been currently more studied (Table 3).

Table 3. Effects of plasma on pre- and post-harvest plant sustainability.

Plant Species	Plasma Source	Feeder Gas	Treated Stage	Improved Effects	Reference
Pre-harvest tolerance to biotic stresses					
Solanum lycopersicum	RF helium plasma	Helium (He)	Seed	Bacterial wilt resistance	[85]
Glycine max	DBD O_2 and N_2 plasma	Oxygen (O_2) and nitrogen (N_2)	Seed	Diaporthe/Phomopsis fungal resistance	[87]
Solanum lycopersicum cv. Moneymaker and VF010	Plasma-activated water	Ambient air	Seedling	Bacterial leaf spot resistance	[88]
Pre-harvest tolerance to abiotic stresses					
Brassica napus	He plasma discharge	Helium (He)	Seed	Drought stress tolerance	[84]
Pisum sativum L.	Coplanar DBD plasma	Ambient Air	Seed	Tolerance to zeocinLess DNA damage	[89]
Arabidopsis thaliana	DBD air plasma	Air and helium (He)	Seed	Salt stress tolerance	[90]
Triticum aestivum	Low-pressure DBD plasma with Ar/O_2 and Ar/air gases	Argon (Ar)/oxygen (O_2) and argon (Ar)/air mixture	Seed	Tolerance to cadmium (Cd)	[91]
Hordeum vulgare	Plasma-activated water	Nitrogen (N_2)	Seed	Tolerance to low temperature and hypoxia	[92]
Solanum lycopersicum	Air Plasma Jet	Air	Seed	Tolerance to PEG (polyethlene glycol)-mediated drought stress	[93]
Post-harvest sanitation					
Lactuca sativaBrassica oleracea sp. Capitata	Cold oxygen plasma lamp (Photoplasma, Model: Induct ID60)	Oxygen (O_2)	Lettuce and cabbage vegetables	*L. monocytogenes* biofilm removal	[94]
Blueberries	AC plasma jet	Air	Blueberry fruits	Removed microbial contamination	[95]
Strawberries	Plasma-activated water	Argon (Ar)/oxygen (O_2) mixture	Strawberry fruits	Removed microbial contamination	[96]
Cucumis melo L. var. Reticolatus cv. Raptor	DBD plasma	Air	Melon fruits	Removed microbial contamination	[97]
Red chicory	DBD plasma	Air	Chicory vegetables	Reduced microbial contamination	[98]
Lycopersicum esculentum Mill.	Intermittent corona discharge plasma jet	Air	Cherry tomato fruits	Reduced microbial contamination and increased shelf life	[99]
Apple cv. Granny Smith	Low-pressure plasma (expanded plasma cleaner PDC-001/002)	Argon (Ar), nitrogen (N2), oxygen (O2), and Argon–oxygen (Ar-O2)	Apple fruits	Removed microbial contamination	[100]
Post-harvest quality					
Actinidia deliciosa cv. Hayward	DBD plasma	Air	Kiwi fruits	Improved visual quality and extended storage life	[101]
Agaricus bisporus	Plasma jetPlasma-activated water	Argon–oxygen (Ar-O2)	Button mushrooms	Reduced microbial contamination and delayed softening	[102]
Radish sprouts	Microwave N_2 plasma	Nitrogen (N_2)	Radish sprout vegetables	Reduced moisture content during storage without changing antioxidant activity or ascorbic acid concentration.	[103]

Table 3. *Cont.*

Plant Species	Plasma Source	Feeder Gas	Treated Stage	Improved Effects	Reference
Mandarins	Microwave N_2, He, N_2 + O_2 plasma	Nitrogen (N_2), helium (He) and nitrogen (N_2)/oxygen (O_2) mixture	Mandarin fruits	Increased antioxidant activity and phenolic content	[104]
Mung bean sprouts	Plasma-activated water	Air	Mung bean sprout vegetables	Reduced microbial contamination without changing polyphenolic and flavonoid contents.	[105]

Several studies have shown improved tolerance to abiotic stress after plasma treatment. Ling et al. [84] treated the seeds of two *Brassica napus* cultivars (Zhongshuang 7, a drought-sensitive cultivar, and Zhongshuang 11, a drought-resistant cultivar) with helium plasma and found that plasma treatment enhanced seed germination under 15% (*w*/*v*) PEG 6000-mediated drought conditions. Similarly, the seeds of two *Arabidopsis* mutants, *gl2* and *gpat5*, were exposed to DBD air plasma, and he seed germination efficiency was assessed under salt stress. Plasma causes structural changes to the mantle layers of the seed coat, which reduces permeability and diminishes the effects of salt stress on seed germination [90]. Upregulation of the drought stress-regulating transcription factor (WRKY) and secondary metabolites in plasma-treated seedlings was reported by Iranbakhsh et al. [106]. More recently, Adhikari et al. [93] demonstrated that cold atmospheric pressure plasma seed priming induces drought stress tolerance in seedlings—improved growth and biochemical alterations were observed in the cold plasma-primed tomato seedlings under 30% PEG-mediated drought stress. Other reports have shown that the plasma-activated water irrigation of barley improves hypoxia and low-temperature stress tolerance [92]. Pollutant soil contamination is a major concern in agriculture; the Air/Ar cold low pressure plasma treatment of wheat seeds reduced the accumulation of Cd during germination. This is because plasma treatment modifies the seed coat and reduces the pH of wheat seeds, resulting in Cd detoxification [91].

Plasma can promote plant tolerance to biotic stressors, such as pathogens and pests. Pathogenic diseases severely damage crop yield and are a major threat to food security. Cold low pressure plasma treatment of tomato seeds reduced bacterial wilt disease (causal agent: *Ralstonia solanacearum*) at the early vegetative stage [85]. Seed-borne pathogens, such as *Fusarium fujikuroi* (Bakanae disease) and *Burkholderia plantarii* (bacterial blight), can also be controlled by cold atmospheric pressure plasma irradiation on rice [107]. Many researchers have reported the inactivation of phytogenic bacteria on seeds and the upregulation of pathogen resistance genes in plants after cold atmospheric pressure plasma exposure [49,87]. Plasma-activated water irrigation induced the tomato plant defense system against *Xanthomonas vesicatoria* (Xv), although antimicrobial effects of the PAW against *X. vesicatoria* were not observed [88]. The induced expression of the PAL transcript upon PAW irrigation may be associated with the induced tomato defense system [88].

Harvesting, storage, and processing are crucial steps in the agricultural system. Food processing involves the transportation, cleaning, sorting, blending, and milling of crops to convert them to food. Technological innovations for the post-harvest storage and food processing stages are required to increase the food security index of the current agricultural system. Cold atmospheric or low pressure plasma is a promising technology to decontaminate and improve the shelf life of fresh and processed food products [108]. Several studies have reported plasma effects on post-harvest storage and food processing (Table 3). Microbial contamination during processing, packaging, and storing is a major problem that decreases shelf life, deteriorates taste, and causes food poisoning. Plasma treatment efficiently reduces the microbial contaminants on fruit, vegetables, and other edible products in a time- or dose-dependent manner, as summarized in a recent review [109]. The antimicrobial potential of plasma is well demonstrated by various cold atmospheric or low pressure plasma sources (gliding arc discharge, cold plasma argon jet, helium jet, microwave-generated plasma, and dielectric barrier discharge (DBD) plasma), microbes (*Erwinia carotovora, Salmonella anatum, Salmonella enterica serovar Stanley, Salmonella enteritidis, Escherichia coli, Erwinia amylovor, Listeria monocytogenes, Clavibacter michiganensis subsp. Sepedonicus, Dickeya solani, X. campestris pv. Campestris, P. atrosepticum, Pectobacterium carotovorum subsp. Carotovorum, Pseudomonas fluorescens, Pseudomonas marginalis*, and *P. carotovorum*), and fresh products (lettuce, tomatoes, carrots, cherries, figs, black peppers, strawberries, onions, radishes, cress, alfalfa seeds, grapes, bananas, and almonds). Studies have also shown that plasma cannot completely eradicate the microbial load but does prevent the microbes from multiplying [109]. An industrial-based DBD prototype efficiently removed the microflora load of fresh cherry tomatoes and prolonged the shelf life during storage [110]. Plasma-processed air can also reduce the microbial loads of fresh fruits/vegetables and packaged foods [111].

In the food processing industry, conventional techniques such as pasteurization, drying, and freezing, and newer physical strategies, such as ultraviolet (UV) irradiation, X-ray irradiation, ozone washing, and high-pressure processing, have been used to maintain food quality. However, these processing techniques have some drawbacks [112]. In plasma-mediated food processing, cold atmospheric or low pressure plasma can sterilize the food without compromising its flavor, odor, color, and prolonged shelf life. These plasma attributes have attracted the attention of food industry researchers. A comparison of different beverage processing techniques found that the plasma method retained the contents of ascorbic, chlorogenic, sinapic, and gallic acids in a tomato beverage, whereas pasteurization and other non-thermal methods resulted in reduced levels of these same acids [113]. Gas-phase plasma maintained the levels of phenolic compounds and hydroxycinnamic acids and reduced the anthocyanin content (23%), suggesting that anthocyanin is susceptible to the reactive oxygen species produced by cold atmospheric pressure plasma in juice [114]. The color and texture of food are very important to consumers, and studies have shown that plasma treatment has only minor (or no) effects on the color and texture of fruits. Misra et al. [115] used a DBD cold plasma source to process packaged strawberries and observed no changes in the firmness or color, but there was a significant reduction in the microbial load. Similarly, the qualitative attributes of fresh-cut fruit (apple and melon) were not affected by plasma treatment under storage conditions [97,116]. Other food qualities, such as pH, acidity, antioxidants, and the contents of soluble sugar and vitamins, have also been investigated after plasma treatment. About pH, the pH changed due to the reactive oxygen species generated on food after plasma treatment. On the other hand, the pH did not change after plasma treatment because of the buffering capacity of the liquid in living tissue and the physiological activity of removing the acid from the surface [117]. The soluble sugar content is important for the taste of fruit and their juices cold atmospheric pressure plasma reduced the fructose and glucose contents and increased the sucrose content in fruit juices [118,119]. This is because the reactive species generated by plasma promotes ozonolysis reactions, which breaks the glycosidic bond of oligosaccharides and reduces the sugars via oxidation [119,120]. The vitamin contents of fruit and their juices are stable under plasma treatment [116], while the antioxidant activities of fresh food are variably influenced by cold atmospheric pressure plasma treatments, depending on the food products, plasma sources, treatment conditions, and doses [117].

5. Future Prospects and Conclusions

The effects of cold atmospheric or low pressure plasma on plant growth, development, and sustainability have been verified by abundant experimental data. The accumulated data suggest that cold atmospheric or low pressure plasma may provide a reliable method to reduce the risks associated with global climate change and changing agricultural environments. Changes to the traditional agriculture system and practices are inevitable “modern agriculture” has been used to designate this transition. Indoor agriculture, hydroponic culturing, and smart farming associated with ICT (Information and Communication Technology) are frequently used in modern agriculture. Cold atmospheric or low pressure plasma may also contribute to the technological innovations of modern agriculture. For example, plasma applications in indoor and greenhouse cultivation systems are practically possible. Cold atmospheric or low pressure plasma is environmentally and biologically safe and requires little energy compared to other radiation-based technologies. The search for application ways and area to maximize plasma's advantages should be continued. Recently, plasma-mediated improvements to plant tolerance against abiotic and biotic stresses has drawn great interest because of the influence of climate changes on agriculture. Conventional gene editing strategies are limited by safety concerns and the complexity of gene regulation networks, thus presenting an opportunity for cold atmospheric or low pressure plasma applications.

The efficient application of cold atmospheric or low pressure plasma requires experimental evidence and mechanistic studies. Although enhanced plant vitality and development due to plasma treatments have been well documented, evidence for the applied usage of plasma in agricultural fields and facilities is still lacking. Moreover, available experimental data are biased toward laboratory conditions. Thus, field and facility application studies are required. The underlying mechanisms of the plasma effects are also relatively unexplored compared to phenotypic effects discussed here. More information about the modes of plasma action on plant production and sustainability is necessary to optimize and upgrade the plasma systems and applications.

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