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COLD PLASMA APPLICATIONS FOR SEED QUALITY IMPROVEMENT: A REVIEW

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ABSTRACT

Cold plasma (CP) technology is an emerging form of non-thermal, eco-friendly technology that is rapidly being adopted to improve germination rates, overcome dormancy, and improve seedling vigor in a multitude of crops. As opposed to treatments by chemical priming, CP treatments are continuous and do not generally produce any chemical products to leave behind, thus making CP treatment a much better fit in establishing agriculture systems that are more sustainable. CP treatments are commonly but not limited to use dielectric barrier discharge, and radio-frequency discharge with ambient air, oxygen, nitrogen or argon as the feed gas. During CP discharge, there are many different reactive oxygen species (ROS), reactive nitrogen species (RNS) and ultra-violet radiation generated that can initiate changes to seeds at both the surface, and biochemical levels. Cold plasma penetrates into the seed coats reducing morphological characteristics via micro-etching and pore development leading to an improvement in the seed's ability to take-up water and respire. Using spectroscopic methods, it has been demonstrated that there is an increase in the presence of hydrophilic functional groups that enables the seed structures to become more responsive. Cohesively and at the internal level, CP technology produces metabolic changes that are favorable to germination, leading to an increased level of antioxidant enzymes such as catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) that permit germination and/or seedling vigor. In addition, in these roles, activation of these enzymes leads to enhanced abiotic stress tolerance by establishing effective defense responses that the developing embryo can use to endure dynamic environmental pressures. CP alters the hormonal equilibrium from dormancy to germination by tweaking the abscisic acid/gibberellins ratio in the seed. Such physiological changes are usually accompanied by an upregulation of total soluble sugars and proteins, which provide required energy reserves for fast hypocotyl elongation. Thus, the use of cold plasma acts as a variety of triggers between surface state change and complex intracellular/fermentation signaling processing to enhance total crop yield.

***Key words*:** Cold plasma; Seed priming; Seed germination; Seed dormancy; Reactive oxygen species (ROS); Seed coat modification; Antioxidant enzymes; Sustainable agriculture

Introduction

Seed quality is a multifaceted concept encompassing several attributes that determine the performance of seeds during planting or storage (Sevik *et al.*, 2012). It includes physical, physiological, genetic, and other characteristics such as purity, germination capacity, vigour, size, uniformity, health status, and moisture content (Cushman *et al.*, 2019). High-quality seeds ensure better germination, rapid and uniform emergence, and stronger seedling vigour, ultimately contributing to improved crop establishment and yield (Matthews *et al.*, 2012). Seed quality plays a crucial role in both domestic and international seed trade, influencing agricultural productivity and market profitability (Cushman *et al.*, 2000). It is also vital from multiple perspectives—serving as a biosecurity measure, a marketing tool, a requirement

for modern crop production, and an essential component for successful reforestation programs (Sevik *et al*., 2012).

In India, seed productivity remains constrained by the availability of poor-quality seeds, highlighting the need for improved seed production systems and infrastructure (Taku *et al*., 2025). Many Asia-Pacific regions face similar challenges, including limited technical expertise, fragmented production areas, and weak coordination among stakeholders Strengthening seed quality control mechanisms, upgrading storage technologies, and enhancing market information platforms are key steps toward developing an efficient seed sector including seed companies and farming communities (Prasad *et al*., 2017).

Early germination and seedling growth represent critical phases that significantly influence crop establishment and productivity. However, many seeds including those of soybean possess thick or hard seed coats that reduce permeability, delay germination, and cause irregular emergence, resulting in poor seedling establishment (Sayahi *et al*., 2024). Traditional methods to promote germination include physical treatments such as magnetic fields, UV exposure, and hot water soaking, as well as chemical treatments like fungicides and plant hormones. Although effective, these approaches can be labour-intensive, time-consuming, and prone to leaving hazardous chemical residues that pose risks to human health and the environment (Subedi *et al*., 2017)

Cold plasma technology has emerged as a sustainable, eco-friendly alternative with significant potential to enhance seed quality and germination (Biruntha *et al*., 2025). As a non-thermal process utilizing partially ionized gas, cold plasma generates reactive species that modify seed surface properties, improve water uptake, and stimulate internal metabolic processes (Sonawane *et al*., 2020). It can be applied directly to seeds or indirectly through plasma-activated water, both of which rely on reactive oxygen and nitrogen species to break dormancy and induce germination (Thirumdas *et al*., 2018). Additional benefits include effective seed disinfection, pathogen elimination, and improved crop productivity without leaving harmful chemical residues (Thirumdas *et al*., 2018). Nonetheless, challenges remain in optimizing plasma conditions for different seed types, ensuring cost-effectiveness, and developing standardized protocols suitable for commercial adoption (Biruntha *et al*., 2025). Continued research is essential to fully harness the potential of cold plasma in advancing sustainable agriculture.

Fundamentals of Cold Plasma Technology

Plasma, often described as the fourth state of matter, is a partially ionized gas composed of energetic electrons, positively and negatively charged ions, neutral atoms and molecules in their ground or excited states, and a spectrum of emitted photons ranging from ultraviolet (UV) to vacuum-UV radiation (Iseki *et al*., 2010). Its fundamental characteristics are particularly electron density and energy which are shaped by the method of plasma generation and its intended application. Based on thermal behavior, plasmas are broadly divided into hot (thermal) and cold (non-thermal) types. Cold plasma (CP), an artificially generated form, operates at nearly ambient temperatures despite containing electrons with extremely high temperatures (~10,000 K), indicating a lack of thermal equilibrium (Moutiq *et al*., 2019). Cold Plasma typically contains electron energies ranging from 1–10 eV and electron densities around 10^{9} -$10^{15}$$cm^{-3}$, with ionization levels below 10^{-3} Bq. Consequently, most of the gas remains neutral, and the plasma is primarily enriched with reactive radicals and neutral species (Thirumdas *et al*., 2018).

Characteristics and Composition of Cold Plasma

Cold plasma is formed when a strong electric field ionizes a working gas, causing a release of electrons and elevating electron density to 10^{11}–10^{16} cm^{-3}. Rapid electron–molecule collisions produce an array of reactive oxygen species (ROS) and reactive nitrogen species (RNS), such as O_2^-, OH^-, H_2O_2, $^1O_2$, O_3, NO, NO_2, and $ONOO^-$ (Zhang *et al*., 2021). The composition and quantity of these species depend heavily on the gas type, plasma configuration, voltage, frequency, and gas flow. For instance, adding oxygen to helium or argon encourages ozone formation, whereas air plasmas produce higher amounts of RNS due to abundant nitrogen (Stoffels *et al*., 2002). These variations in plasma chemistry complicate standardization and hinder comparison across studies because different devices generate different reactive species profiles (Zhang *et al*., 2021).

Key Components of Cold Plasma

Electrons are the most energetic and mobile species, initiating ionization, excitation, and dissociation of gas molecules (Thirumdas *et al*., 2018). Ions support conductivity and can interact with seed cell membranes, influencing permeability (Moutiq *et al*., 2020). Neutral atoms and excited molecules participate in secondary chemical reactions, while ROS and RNS such as O_3, OH^-, NO, and $ONOO^-$ play essential roles in regulating seed metabolism and stress signaling (Jiang *et al*., 2014). Ultraviolet (UV) and Vacuum ultraviolet (VUV) radiation further contribute by breaking molecular bonds, aiding in

sterilization and modifying the seed surface (Niemira *et al*., 2012).

Cold Plasma Generation Techniques

Several technologies are available to generate cold plasma, including Atmospheric Pressure Plasma (APP), Dielectric Barrier Discharge (DBD), Glow or Radio-Frequency Discharge (GD/RFD), and Corona Discharge (CD) (Thirumdas *et al*., 2018) Fig. 1. Atmospheric Pressure Plasma systems operate at atmospheric pressure and often utilize inert gases like helium combined with reactive additives such as oxygen or water vapor. Their non-thermal nature and high flow capacity make them suitable for agricultural applications (Patil *et al*., 2014). DBD systems operate with pulsed voltages applied between two electrodes, one of which is coated with a dielectric layer. This prevents arc formation, ensuring uniform discharge and minimal heating (Moutiq *et al*., 2020). Glow discharge or RF systems operate under reduced pressure and provide extremely uniform plasma, powered by DC, RF, or microwave sources (Niemira *et al*., 2012). Although Corona Discharge operates at atmospheric pressure and is easy to generate, its localized heating and spatial non-uniformity make it less suitable for consistent seed treatment (Sharma *et al*., 2022).

Mode of Action of cold plasma in Enhancing the seed quality

Cold plasma has been reported to improve seed germination, accelerate seedling growth, and enhance resistance against pathogens across a variety of crop species (Sehrawat *el al*., 2017). These beneficial effects are primarily attributed to mechanisms such as modification of seed coat permeability, activation of enzymatic antioxidant systems, regulation of phytohormones, and decontamination of seed-borne microorganisms (Niemira *et al*., 2012). Furthermore, CP treatment has shown potential in mitigating the adverse effects of abiotic stresses, thereby contributing to improved seed vigor and field establishment (Mitra *et al*., 2014).

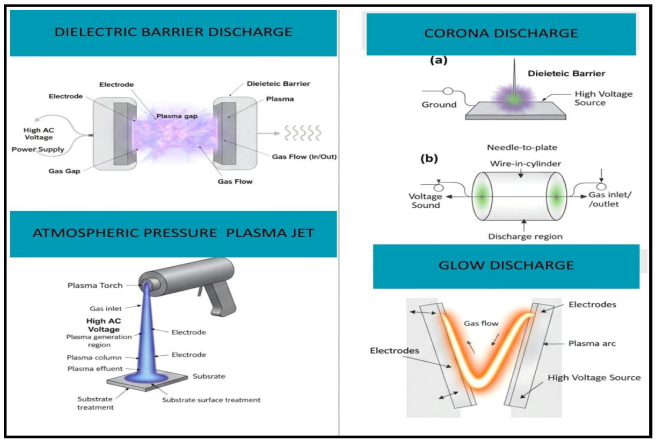


Fig. 1: Methods of generation of cold plasma.

Modification of Seed Coat Structure

Cold plasma induces substantial physical and chemical alterations on seed surfaces. Through micro-etching by ROS, ions, and UV photons, CP creates micro-cracks, pits, and grooves that increase surface roughness and porosity. These microstructural changes significantly improve water uptake and gas diffusion, accelerating imbibition and metabolic activation. (Roy *et al*., 2025)

Increased Wettability and Hydrophilicity

CP reduces the surface contact angle by introducing polar functional groups such as –OH and –COOH, thereby increasing hydrophilicity. Enhanced wettability results in more rapid and uniform water absorption, which is essential for dormancy alleviation and germination onset (Jiang *et al*., 2014).

Improved Oxygen Exchange

The plasma-etched micro channels facilitate enhanced oxygen penetration into internal tissues. Since oxygen is critical for aerobic respiration during early germination, this improved gas exchange boosts energy production and supports stronger seedling emergence (Thirumdas *et al*., 2018).

Seed Quality Parameters Affected by Cold Plasma

Seed quality encompasses a range of attributes, including germination potential, seed vigour, physiological performance, and biochemical composition, all of which collectively determine successful crop establishment. Cold plasma (CP) treatment has emerged as an effective non-thermal approach capable of modulating these seed quality parameters through physical and biochemical alterations at the seed surface and internal tissues (Thirumdas *et al*., 2018). The interaction of ROS and RNS generated during CP exposure induces changes in membrane permeability, enzymatic activity, and metabolic processes, thereby influencing key aspects of seed performance (Finch-Savage *et al*., 2015). Consequently, CP treatment has been widely investigated for its role in enhancing germination, improving seed vigour, and regulating physiological and biochemical responses in seeds (Shilpa *et al*., 2024).

Germination and viability

Cold plasma (CP) treatment has demonstrated excellent potential in enhancing seed germination, and seedling emergence as well as overall growth of diverse crop species. It has been reported that treatment of CP caused a significant improvement in germination percentage, seedling vigor, and early vegetative growth

Table 1: Key Enzymes and Genes under cold plasma treatment in seeds.

Mechanism	Enzymes Involved	Genes Involved	References
Starch Breakdown	α-Amylase	αAmy3, Amy1A	Li *et al.*, (2016);
Lipid Mobilization	Lipase	-	Li *et al.*, (2016)
Protein Mobilization	Protease	-	Li *et al.*, (2016)
Antioxidant Defense	SOD, POD, CAT, PPO	SOD1, CAT1, APX1	Jiang *et al.*, (2014); Subham *et al.*,(2017)
ROS Signaling	-	Rboh	Stoffels *et al.*(2002)
Photosynthesis	-	Chlorophyll biosynthesis genes	Ling*et al.*, (2013);

(De Groot *et al.*, 2018). These advantages are mostly through alterations in seed surface properties via CP, resulting in enhanced water absorption and reduced water contact angle to initiate germination more quickly (Li *et al.*, 2016). (ROS) and (RNS) generated during CP atmospheric dielectric discharge play a crucial role in dormancy breaking, as well as initiation of the early metabolically active processes (Sehrawat *et al.*, 2017). Furthermore, several reports have shown these beneficial effects from plasma treatment can be maintained over time, with some reports showing increases in germination several months after treatment (De Groot *et al.*, 2018).

Seed Coat Modification and Enhanced Water Uptake

One of the main ways CP enhances germination is by modifying the seed coat structure and chemistry. Ions, UV photons, and ROS from plasma produce micro-etching to initiate cracks, pores, and surface roughness, greatly improving the seed coat's porosity and hydrophilicity, which in turn allowed for more rapid and efficient water uptake in treated seeds (Filatova *et al.*, 2020). Soybean seeds treated with CP were found to take up water more quickly, required less imbibition time, and exhibited improved germination rates (Ling *et al.*, 2014). Other studies on surface modification of seeds have occurred with wheat seeds, in which seed permeability improved and metabolic activation accelerated (Jiang *et al.*, 2014). DBB-treated carob seed, which usually have extremely hard seed coats, demonstrated increased water absorption and faster germination after CP treatment (Sayahi *et al., 2024*).

Improved Germination Rate and Uniformity

Cold plasma dramatically promotes germination and increases uniformity that is necessary to achieve field establishment. In wheat, studies have reported 20–30% increase in germination per cent and significant decrease in MGT as a result of CP treatment (Jiang *et al.*, 2014). Analogous changes in germination index was also reported for tomato, low-pressure CP improved germination index and reduced seedling emergences through increased metabolic activity (Santosiang *et al.*, 2014).

Enhanced Metabolism and Hydrolytic Enzyme Activation

CP activates primary hydrolytic enzymes for reserve mobilization, which is a vital process of the early period of seed development. CP increases activity of á-amylase which hydrolyses the starch substrate into available sugars. This phenomenon would be related to the increased GA_3 levels induced by the ROS signal. Increased protease and lipase activities have also been described to justify the enhancement in protein hydrolysis and lipid mobilization, mainly in oilseeds like soybean and carob (Sayahi *et al.*, 2024). These enzymatic reactions act together and contribute to the rapid germination and growth. (Table 1).

Phytohormone Regulation

In addition, plasma-induced ROS function as important signaling molecules to control phytohormones homeostasis. Usually CP treatment elevates the content of GA_3 and decreases ABA, which help break dormancy and activate metabolism (Fig. 2). Such hormonal changes were previously reported in Arabidopsis and have been clearly correlated with an accelerated germination and a better early seedling growth (August *et al.*, 2023)

Antioxidant Defense Activation

CP-induced a slight oxidative burst leading to stimulation of the antioxidant defence. Enzymatic antioxidants (SOD, CAT, APX and GR) are typically unregulated, but also non-enzymatic antioxidants

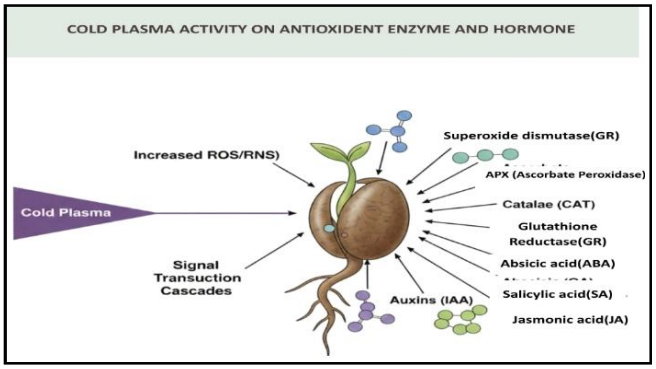


Fig. 2: Activation of plant hormones by cold plasma.

Table 2: Various vigour index parameter affected by cold plasma.

Aspect of Seedling Vigor	Observed Effects of Cold Plasma (CP)	Key Findings / Magnitude of Change	References
Root Growth Stimulation	Increased root length, dry weight, and branching	Root dry weight increased by ~9% in groundnut; longer and more branched root systems in cereals	Li *et al.*, 2016 Stolárik *et al.*, 2015
Shoot Growth Enhancement	Increased shoot length, biomass, hypocotyl elongation, and leaf expansion	Shoot biomass increased by ~11% in groundnut; enhanced shoot/root length in soybean and wheat	Li *et al.*, 2016 Dhayal *et al.*, 2006 Ling *et al.*, 2014
Biomass Accumulation	Higher fresh and dry weight of seedlings	Improved enzyme activity, reserve utilization, and photosynthetic efficiency; strong biomass increase in carob after DBD plasma	Jiang *et al.*, 2014 Sayahi *et al* .,2024 Li *et al.*, 2016
Seedling Vigor Index (SVI)	Significant increase in SVI due to improved germination and growth	SVI increased significantly; 30–50% increase reported in lentil and soybean	Li *et al.*, 2016; Bormashenko *et al.*, 2012
Seed Coat Modification	Increased permeability and surface oxidation	Enhanced water imbibition and faster metabolic reactivation	Li *et al.*, 2016
Hormonal Regulation	Increased GA*f* and decreased ABA levels	Accelerated germination and elongation processes	Souza *et al.*, 2017
Antioxidant Capacity	Increased SOD, CAT, and POD activities	Improved protection against oxidative stress during rapid early growth	Subham *et al* ., 2017
Reserve Mobilization	Faster breakdown of starch, proteins, and lipids	Early energy supply for vigorous seedling establishment	Li *et al.*, (2016)
Field-Level Performance	Better stand establishment and yield	Yield increase of 10–13%; reduced reseeding and improved crop uniformity	Li *et al.*, 2016; Selcuk *et al.*, 2008

ascorbate, glutathione and phenolic accumulate to sustain redox homeostasis (Table 1). These responses are not only stress-related, but also play positive roles in metabolic functions for germination (Li *et al*., 2016) (Fig. 3).

Enhancement of the Germination Indices, and Vigor Index of Seedlings

In addition to improvement in germination percentage and MGT, CP has also been reported to increase germination related attributes such as Germination index (GI), seedling vigor index (SVI) and root &shoot length. For example, CP has led to high root and shoot growth in chickpea seeds (Pathan *et al*., 2023). Soybean and wheat registered relatively high SVI values which could be due to more reserve mobilization as well as an efficient metabolism (Xing & Hu *et al*., 2024).

Surface Chemistry, Wettability and Long-Term Behaviour

For Bambara groundnut, CP treatment also improved germination from 75.5 to 93.3% and decreased MGT from 8.57 to 6.14 days (Taku *et al*., 2025). WCA also significantly decreased by plasma treatment with highly improved wettability from 114.0° to 44.0°; even partial hydrophilicity could be preserved >60 days (Li *et al*., 2016). Chemical composition, as determined by X-ray Photoelectron Spectroscopy (XPS) method showed enhanced O/C and N/C ratios. Augmented water imbibition and metabolic activation was also confirmed by improved EC in the treated seeds depicting strong physiological status (Zahoranová *et al*., 2016). A number of such structural and chemical effects are maintained over weeks, as a result of the slow aging of lignin and cell.

Seed dormancy

Treatment with CP breaks seed dormancy by triggering micro-etching of the seed coat, which facilitates

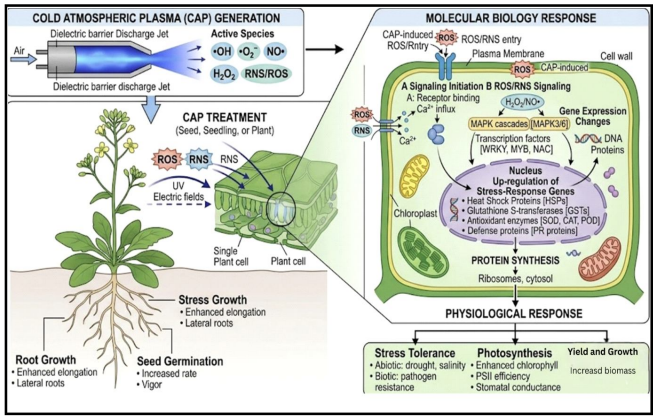


Fig. 3: Application of cold plasma on molecular biology and on physiological parameters.

Table 3: Various microorganism affected by cold plasma.

Crop / Seed Type	Target Pathogen(s)	Treatment Summary & Key Findings	Reference
Rice	*Helminthosporiumoryzae* (Brown Spot)	20 kV for 10 min significantly reduced seed infection and improved germination to 93.33%.	Abeysingha *et al.*, (2025)
Soybean	*Colletotrichum sp.*, *Rhizopus* sp. *Aspergillus niger*	10 kV for 15 min reduced infection by 37%; significantly improved field emergence.	Jiang *et al.*, (2014)
Wheat & Maize	*Fusarium culmorum*, Native fungal flora	Significant reduction in fungal load (1-2 log units) with improved seedling vigour.	Zahoranová *et al.*, (2016)
Tomato	*Ralstonia solanacearum* (Bacterial Wilt)	Increased disease resistance by 25% and enhanced nutrient uptake (Ca and B).	Shivaraju *et al.*,(2023)
Buckwheat	*Alternaria sp*, *Epicoccum sp*	120s exposure reduced fungal frequency to levels comparable to chemical sterilization.	Mravlje *et al.*, (2021)
Barley	*Fusarium graminearum*	6-10 min treatment reduced Mycotoxin (DON) concentration by up to 54.4%.	Filatova *et al.*, (2020)
Chickpea	Natural microbiota	2-5 min exposure achieved 1-2 log reductions in surface microbial load.	Mitra *et al.*, (2014)

water entry and oxygen penetration. The ROS and RNS produced upon plasma treatment also function as signalling molecules to induce the metabolic wake-up of dormant seeds. CP regulates hormone homeostasis; it promotes GA_3 accumulation and inhibits ABA level, which is favourable for seed germination. Both the physical and biochemical effects act to decrease dormancy intensity and enhance more rapid, uniform germination without chemical treatments (Stolárik *et al*., 2015).

Seed vigour is an essential component of seed quality that determines the ability of seeds to germinate rapidly, emerge uniformly, and establish strong seedlings under a wide range of environmental conditions, including stress situations. Unlike standard germination, it reflects actual field performance and is influenced by physiological and biochemical factors such as membrane integrity, enzyme activity, and efficient reserve mobilization (Fig. 2) (Cushman *et al*., 2019). In recent years, cold plasma (CP) has emerged as an innovative and eco-friendly technique to enhance seed vigour. CP generates (ROS and RNS) that induce physical and biochemical changes in seeds, including improved seed coat permeability, enhanced water uptake, and activation of metabolic processes (Li *et al*., 2016). These reactive species also regulate phytohormones like gibberellic acid (GA_3) and abscisic acid (ABA), and stimulate antioxidant and hydrolytic enzymes, thereby promoting faster germination, better stress tolerance, and improved seedling growth (Jiang *et al*., 2014).

Enhanced Seedling Vigor Induced by Cold Plasma

Vigor at early seedling stage is an important factor affecting crop establishment, early growth and final yield. It includes characteristics like root and shoot growth, dry matter content and indices that are combinations of these traits e.g. SVI (Bassel *et al*., (2015)). In the past several years, cold plasma (CP) has been introduced as an eco-friendly method for seed priming that can improve significantly seedling vigor (Shilpa *et al*., 2024). It has been shown to have beneficial effects in various crops like soybean, wheat, chickpea, tomato groundnut, carob and lentil (Table 3). Vigor increase is due to a set of physical changes in the seed coat (that are generated), metabolic triggers and molecular signaling pathways stimulated by plasma-derived reactive species (Jiang *et al*., 2014).

Root and Shoot Growth Stimulation

Cold plasma also has a marked effect on root and shoot development, resulting in healthier seedlings with increased resistance to stress. In groundnut, the root dry weight of CP-treated seedlings increased by 9% more than those of untreated control (Li *et al*., (2016)). Increased root length can lead to improved water and nutrient uptake with conferencing greater plant efficacy under stress conditions and increased yield capacity (Jiang *et al*., 2014). Positive effects have also been observed in wheat, barley, and safflower in terms of longer and more branched root system using CP stimulated seeds (Velez *et al*., 2025). Shoot growth also could be promoted by CP application; groundnut seedlings show an 11% increase in shoot biomass (Li *et al*., 2016), and significant increases rooted hypocotyl elongation, leaf expansion were recorded for cowpea (Velez *et al*., 2025) as well. Shoot and root lengths of soybean (Ling *et al*., 2014) and wheat (Jiang *et al*., 2014) seedlings were also enhanced

Biomass Accumulation and Metabolic Enhancement

It is evident that seedlings sprouting from CP-treated seeds regularly exhibit increased fresh and dry weight. Indeed, this improvement involves stronger enzyme function, improved use of stored reserves, and better

photosynthetic efficiency. CP priming in tomato plants turned on growth-boosting genes and metabolic routes, thereby producing a heavier seedling mass (Jiang *et al*., 2014). It was clear that Carob seeds, which are usually held back by tough seed coats, displayed strong biomass growth after DBD plasma exposure, thanks to better oxygen and water flow (Sayahi *et al* ., 2024). As a result, plasma-induced oxidation of hydrophobic surface compounds cuticular waxes, suberin, condensed tanins, lignin and enhances water absorption and promotes metabolic reactivation.

Improved Seedling Vigor Index (SVI)

Cold plasma dramatically increases the SVI a key measurement of early growth capacity. The germination rate and root/shoot length were higher in plasma treated groundnut seeds, which significantly increased the SVI (Li *et al*., 2016). Similarly, wheat, chickpea, soybean, lentil also manifested a considerable increase of SVI when their germination was synchronized and early growth improved- the SVI increased by 30-50% in the case of lentil and soybean (Bormashenko *et al*., 2015).

Underlying Mechanisms of Vigor Enhancement

CP-mediated vigour enhancement is due to a number of physiological and biochemical processes, including higher seed coat permeability which promotes water uptake and is associated with enzyme catabolic activation (Li *et al*., 2016) and hormonal changes involving an increase in GA_3 and a decrease in ABA that induce germination and elongation processes (Cushman *et al*., 2019). Cold plasma also amplified antioxidant capacity with increased SOD and CAT that supports cell protection during rapid early growth (Subham *et al*., 2017) and improved reserve mobilization that accelerates the breakdown of starch, proteins, and lipids, thereby ensuring an early supply of energy during germination (Li *et al*., (2016)).

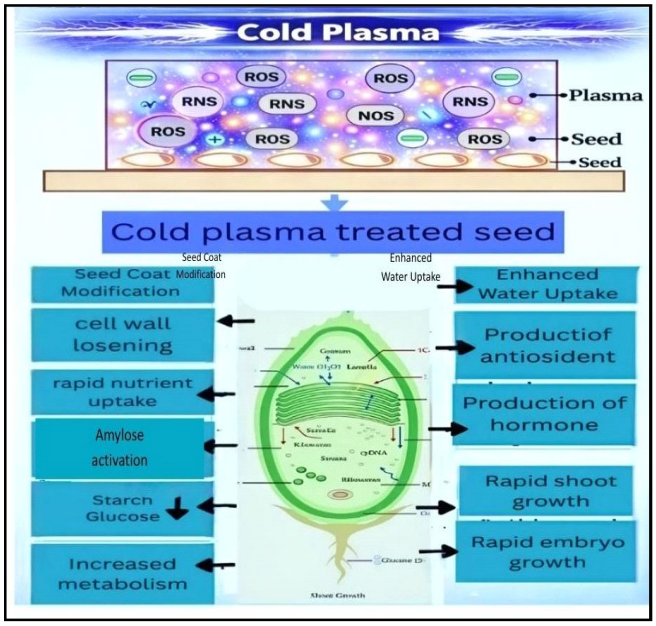


Fig. 4: Morphological and biological changes occurring inside seed by action of cold plasma.

Physiological and biochemical changes

The Cold Plasma Treatment activates a variety of biochemical and physiological changes in seeds and seedlings, which is beneficial to the early growth, metabolic activation, and crop performance as a whole (Fig. 4). These effects are observed at several developmental stages early seedling establishment to fructification and final yield demonstrating the long-lasting positive impact of plasma-activated priming of seeds. (Karimi *et al*., 2024)

Early Seedling Stage: Biomass Accumulation and Metabolic Activation

At the seeding stage, it is possible to see that shoot and root DW after 7 days are indirectly affected by initial effects of CP treatment on biomass accumulation. A higher seedling dry weight in plasma-treated seeds (11% increase for shoots and 9% for roots) was observed, when exposed to a 120 W plasma discharge. These changes suggest that mobilization of storage-accumulated reserves and the activation of metabolic routes required for vigorous early growth are enhanced (Chen *et al*., 2020). The increase root growth facilitates water and nutrient uptake, while the higher shoot weight prepares the plant for proper photosynthesis activity in coming end of season (Karimi *et al*., 2024).

Physiological Changes at the Fruiting Stage

In order to study the physiological changes at the later stages, the major leaf traits, namely leaf area, thickness, SPAD values (which denote chlorophyll content), nitrogen concentration, water content, and total dry biomass, were analyzed. All the parameters except water content showed a positive effect of plasma treatment. The increase in leaf area was 15%, thickness 7%, SPAD readings 9%, nitrogen concentration 3%, and total dry biomass 12% (Velez *et al*., 2025). The enhancements indicate that the CP-treated plants are oxygen releasing and sequestering at higher rates, which is associated with more chlorophyll, better leaf structure, and more nitrogen assimilation. Such characters lead to faster canopy formation and more productive source–sink relations during the reproductive growth period. (Dufour *et al*., 2021).

Cold plasma on seed microbial activity

Seed-borne pathogens, including bacteria and fungi,

pose significant threats to seed quality, storage life, and crop establishment, often leading to reduced germination and field infections (Niemira *et al*., 2012). Its broad-spectrum antimicrobial activity is primarily attributed to the synergistic effects of reactive oxygen and nitrogen species (RONS), ultraviolet radiation, charged particles, and transient electric fields, making it an eco-friendly alternative to conventional chemical treatments (Selcuk *et al*., 2008).

The microbial action of CP is mediated through several pathways, including the lipid peroxidation of microbial cell membranes, which leads to intracellular leakage and cell death; (Simoncicova *et al*., 2019). Additionally, CP causes oxidative damage to essential proteins, enzymes, and nucleic acids, effectively halting microbial replication (Zahoranová *et al*., 2016). Electron microscopy has confirmed substantial physical damage to exposed microbes, such as cell wall breakage and cytoplasm shrinkage, yet the low-temperature nature of CP ensures that these detrimental effects remain restricted to the seed surface, leaving internal tissues and embryos intact (Selcuk *et al*., 2008).

CP has demonstrated high sterilization efficacy across diverse crops, including tomato, wheat, maize, lettuce, and pepper, achieving microbial reductions of 2–5 log units depending on treatment parameters. Notably, CP is effective against highly resistant fungal spores from genera such as *Fusarium*, *Aspergillus*, and *Alternaria*. (Table 3) Reactive species like ozone and nitric oxide diffuse through resistant spore coats to cause oxidative structural failure, effectively increasing seed storage longevity and sanitation (Zahoranová *et al*., 2016).

A unique advantage of CP is its ability to treat seeds with irregular surface morphologies where pathogens often hide in micro-niches inaccessible to liquid chemicals. Reactive plasma species can penetrate these areas to eliminate adherent microbial populations without causing morphological deterioration (Jiang *et al*., 2014). Furthermore, advanced CP systems can be tuned to target specific pathogens while leaving beneficial microbial communities or internal seed structures unharmed, facilitating safer seed handling and international trade (Vatchev *et al*., 2025).

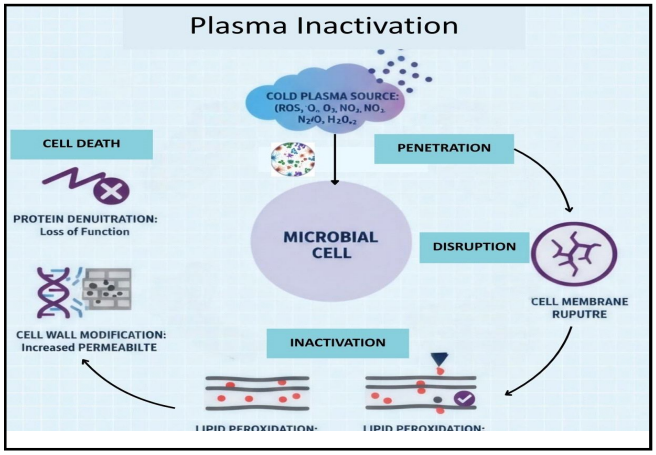


Fig. 5: Microbial deactivation by cold plasma.

The sterilization efficacy of cold plasma (CP) is a synergistic process involving physical and chemical stressors that target the structural and functional integrity of pathogens. The following steps are the way by which cold plasma deactivates the microbial activity of microbes.(Fig 5)

Physical Etching & Disruption: Charged particles and ions in the plasma discharge bombard the microbial surface, a process known as etching. This erodes the outer layers of fungal spore coats or bacterial cell walls, creating micro-pores and fractures that compromise the pathogen's primary defense (Zahoranová *et al*., 2016).

Oxidative Membrane Damage: Reactive Oxygen and Nitrogen Species (RONS), such as hydroxyl radicals and ozone, initiate lipid peroxidation in the cell membrane. This chemical degradation leads to a loss of membrane semi-permeability, resulting in the leakage of essential intracellular contents like proteins and electrolytes (Zahoranová *et al*., 2016).

Internal Inactivation: Once reactive species penetrate the cell, they cause localized oxidative stress. This halts microbial survival by oxidizing sulfhydryl groups in enzymes and damaging nucleic acids. Concurrently, UV-C radiation emitted by the plasma causes DNA strand breaks and thymine dimers, preventing replication (Niemira *et al*., 2012)

Irreversible Cell Death: The cumulative effect of surface erosion, membrane collapse, and internal biochemical failure results in total inactivation. While these effects are lethal to surface-dwelling microorganisms and highly resistant spores, the seed's internal embryo remains protected due to the low-temperature, surface-limited nature of the treatment (Filatova *et al*., 2013).

Beyond its efficacy, CP offers significant environmental and operational benefits by reducing reliance on chemical fungicides, thereby preventing pathogen resistance and environmental pollution. Because it leaves no toxic residues or mutagenic effects, CP is ideally suited for organic and sustainable agricultural systems (Rahman *et al*., 2025). Collectively, these features establish cold plasma as a vital, environmentally benign technology for improving the microbial safety of seeds and supporting sustainable crop production (Selcuk *et al*., 2008).

Table 4: Applications of Cold Plasma Technology in Different Crop Seeds.

Crop	Cold Plasma Treatment & Conditions	Major Effects on Seeds/Plants	Physiological, Biochemical & Molecular Changes	Reference
Wheat (*Triticum aestivum.*)	50 Hz, 60 s	Improved germination, seedling length, biomass; pathogen inactivation	Increased chlorophyll, α-amylase activity; upregulation of CAT1, SODI, APX1; improved surface wettability	Zahoranová *et al.*, 2016
Maize (*Zea mays*)	Atmospheric CP	20–30% higher germination; improved drought tolerance	Enhanced POD and SOD activity; increased proline and soluble sugars; activation of ROS-scavenging and cell-wall genes	Randeniya *et al* .,2015
Bell Pepper (*Capsicum annuum*)	LTAP	Germination increased from 45% to 88%; >95% fungal reduction	Increased CAT and POD; downregulation of NCED; upregulation of GA3ox genes; improved seed coat permeability	Mitra *et al.*, 2019
Groundnut (*Arachis hypogaea*)	120 W, 3 min	Improved biomass, leaf traits; ~10% yield increase	Higher α-amylase; reduced MDA; upregulation of LEA, DREB, APX genes	Li *et al.*, 2016
Tomato (*Solanum lycopersicum*)	50 W, 3 min	>90% microbial reduction; germination up to 98%; enhanced vigor	Increased chlorophyll, biomass; porous seed surface; activation of PAL, CHI, PR-1 genes	Shivaraju *et al.*, 2023
Mung Bean (Vigna radiata)	Atmospheric CP	Faster germination; improved seedling vigor	Increased α-amylase, protease, POD; higher SOD and CAT; reduced ROS and electrolyte leakage	Subham *et al* ., 2017
Barley (*Hordeum vulgare*)	3–5 min	Improved imbibition, early germination, seedling length	Increased CAT and POD activity; reduced water contact angle; improved oxidative stress management	Puac *et al.*, 2014
Chickpea (*Cicer arietinum*)	Atmospheric CP	Improved germination and drought tolerance	Higher proline, membrane stability index; increased SOD and APX activity	Vélez *et al.*, 2025
Soybean (*Glycine max*)	Atmospheric CP	Reduced fungal infection; improved seedling dry weight and leaf area	Upregulation of PR proteins and HSPs; enhanced systemic resistance	Filatova *et al.*, 2013
Lentil (*Lens culinaris*)	2–4 min	Enhanced germination under salinity; longer seedlings	Increased soluble sugars, betaine; upregulation of SOS1 and NHX1 genes	Ouf *et al.*, 2015
Lettuce (*Lactuca sativa*)	Atmospheric CP	Improved germination synchronization; reduced microbial load	Preservation of chlorophyll and antioxidants; extended shelf life	Niemira *et al.*, 2012
Spinach (*Spinacia oleracea*)	Atmospheric CP	Improved seed sanitation and photosynthesis	Higher Fv/Fm values; improved nutrient-use efficiency and stomatal function	Jiang *et al.*, 2014

Applications of cold plasma technology in different crop seeds

Cold plasma has been the focus of much research and application in past years for many types of crop seeds (e.g., oilseeds including sunflower, mustard; vegetables such as tomato, lettuce, and spinach; legumes including soybean and chickpea; cereals including wheat, rice, maize). (Table 5) The technology has been proven effective in enhancing tolerance to environmental stress, enhancing seedling vigor, surface pathogen eradication in addition to increasing the percentage germination of seeds. These benefits are achieved without the use of hazardous chemicals, and allows cold plasma to provide an alternative to the conventional seed treatments.

Wheat (*Triticum aestivum* L.):

In wheat, CP treatment not only improves germination by stripping off hydrophobic seed-surface waxes and facilitating water penetration, but also decreases pathogen (e.g., Fusarium) loads. It promotes the seedling growth, chlorophyll and amylase activity

coupled by up-regulation of antioxidant and photosynthetic genes (CAT1, SOD1, APX1) to enhance stress tolerance (Zahoranová *et al.*, (2016)).

Maize:

It was also found that cold plasma (CP) improved maize germination by 20–30%, conferred beneficial drought tolerance mechanisms perhaps via enhanced stomatal regulation and protective metabolites, or in terms of increased activity of induction of antioxidative enzymes including POD and SOD. CP also induced the expression of ROS-scavenging and cell-wall-strengthening genes, which showed stronger early growth under stress and enhanced the whole-plant yield.(Randeniya *et al.*, (2015))

Bell pepper:

Cold plasma (CP) technology has exhibited vast applications in many field crops, including enhancement of germination, seed vigour, tolerance to stress and control over pathogens. In bell pepper, it was found that low temperature of atmospheric plasma enhanced the germination percentage from 45% to 88%, as well as decreased the Aspergillus contamination by greater than 95% (Mitra *et al.*, (2019)). The promotion of peroxidase and catalase activity also contributed to the release of seed dormancy through modulation of an oxidative and hormonal homeostasis. CP also increased seed-coat permeability and modulated ABA–GA pathways, with downregulation of NCED and upregulation of GA3ox favoring embryo growth.

Groundnut:

In groundnut, it was concluded that germination potential, seedling emergence, biomass and chlorophyll content were enhanced due to plasma treatment. Pods and seed yields increased about 10% with the application of 120 W for 3 min. These benefits were also related to increased α-amylase activity and decreased lipid peroxidation (decreased MDA) expression of stress-induced genes, such as LEA, DREB and APX in the loquat (Li *et al.*, 2016).

Tomato:

Seeds of tomatoes were also well responsive of plasma exposure. A demonstration that a 50 W exposure for 3 min reduced bacteria and fungi load by over 90% and increased germination to over 98%, with better seedling vigor. SEM and FE-SEM images indicated that seed surface was more porous, which can facilitate water absorption. Treated seedlings had more biomass, chlorophyll content and survival than those in 60 days storage. Gene-expression analyses confirmed the activation of PAL, CHI and PR-1 mRNAs indicative of systemic acquired resistance (Shivaraju *et al.*, (2023).

Mung bean:

CP in mung bean hastened germination and mobilization of nutrients. An increased α-amylase, protease, POD, SOD and CAT activity with decrease in electrolyte leakage, reduced ROS level indicating the potential for inducing tolerance to stress and improving field viability. (Subham *et al.*, 2017).

Barley:

Barley exhibited the greatest water uptake and germination rate and highest seedling length after plasma treatment. Treatments of 3 to 5 min increased the wettability and antioxidant enzyme activity especially, CAT and POD that facilitated early seedling growth (Puac *et al.*, 2014).

Chickpea:

Chickpea showed a significant increase in drought tolerance. The seeds treated with plasma had greater proline accumulation, enhanced membrane stability, and more active SOD and APX by performance measures developed with water constraints (Vélez *et al.*, 2025).

Soybeans:

In soybeans, CP reduces fungal pathogens *Rhizoctonia solani* and *Fusarium* spp., but increased the dry weight and leaf area of seedlings. Indicating improved systemic resistance, PR proteins and HSPs were upregulated (Filatova *et al.*, 2013).

Lentils:

Lentils received the positive benefits of increased germination rate under salinity stress, and also increased both osmoprotectants as well as chlorophyll levels. The CP treatment led to the up-regulation of salt-tolerance genes, SOS1, and NHX1 (Ouf *et al.*, 2015).

Lettuce:

Lettuce seeds increased germination uniformity, while the leaves showed a reduction in spoilage with plasma treatment, which retained chlorophyll and antioxidants (Niemira, 2012). Spinach showed improved seed sanitation, increased photosynthetic efficiency (Fv/Fm), positively affected stomatal function, and improved water-use efficiency and post-germination growth (Jiang *et al.*, 2014).

Future prospects for using cold plasma technology to improve seed quality

Agriculture is rapidly moving toward the acute problems of climate change, growing populations, and cleaner, more sustainable practices. Cold plasma technology has become a viable, environmentally-friendly

tool to enhance seed performance and contribute to more resilient crop production in this regard. As a cool, ionized gas abundant in various forms of reactive molecules, cold plasma will improve seed germination, reduce disease, and fortify plants against environmental stresses.

Crop-Specific Plasma Recipes

The response of seeds to cold plasma treatment varies significantly based on their size, structural differences, and sensitivity. Future prospects for cold plasma technology will likely be tailored towards crop specific plasma recipes, which will involve specific concentrations of gas mixtures, time of exposure, and delivery intensity targeted to a specific seed type. Increased crop specificity potential will allow seed laboratories to establish protocols for treatment that maximize germination and vigor for each respective crop, thus establishing some level of standardization for plasma seed treatment globally for specific respective crops.

More Systems for Use in Seed Processing

As the costs decrease, it is envisioned that cold plasma would also be included as standard machinery in seed processing facilities, similar to dryers and seed grading machines that farmers use now. These machines could then be employed to treat large volumes of seeds with no chemical treatments, resulting in high vigor, pathogen free seeds. This will be important as continued push towards organic and low-inputs systems

Building Climate Resilience

One of the most exciting research opportunities is the application of cold plasma to enhance seed resilience to drought, salinity, and heat stress. Initial studies have demonstrated that plasma can modulate some gene expression and metabolic activity patterns to help plants endure stress conditions. In the future, plasma treatments might simply be another method of "priming" seeds to survive adverse climate change conditions.

Complementing Plasma with Advancements

For additional benefits, cold plasma can be utilized together with compatible seed enhancement methods. Seeding techniques like Bio-priming (beneficial microbes) and Nano-priming (nutrient-dense nanoparticles) can be paired together with exposed plasma. Such applications may lead to multifaceted seeds, resulting in faster germination, stronger growth, and fewer external inputs to produce highly optimized precision agriculture systems.

Natural Chemical-Free Method

In light of a national conversation about excessive use of pesticides and fertilizers—cold plasma provides a clean alternative with no residual exposure. Plasma is reliant on air or inert gases, and without significant chemicals, leaves no residual effects on seeds or soil ecosystems. Such practices could meaningfully reduce chemical reliance to improve human health, water quality, and biodiversity, to maintain sustainable and regenerative agriculture.

Enhanced Seed Storage and Shelf Life

Cold plasma has potential in the realm of seed storage in addition to its applications in planting. Cold plasma could extend shelf life and prevent deterioration of seeds, or at a minimum suppress fungal growth, thereby increasing seed viability potential in setting where fungi, moisture and pests are present. This may be especially beneficial for seed banks, wholesale seed suppliers, and farmers who store seeds in between growing seasons.

Furthering Scientific Knowledge

Scientists have taken a deeper look into the biological effects of cold plasma as a means to understand its potential maximum utility, and have done this with - but are not limited to - genomic, proteomic and cellular approaches. Deeper understanding of how plasma affects tissues of seeds at the molecular level may yield more directed and optimized treatments dependent upon crop type, environmental conditions and soil conditions.

Conclusion

Using cold plasma (CP) as a pre-sowing treatment is a convenient, effective, and environmentally safe method for improving germination, seedling vigor (growth), and antioxidant defenses in Iranian soybean cultivars with hard seed coats. Moderate exposure times significantly benefited physiological performance, which included seed germination, root length, shoot length, and biomass. These physiological improvements were closely associated with CP-induced effects on the seed surface by enhancing wettability, roughening and permeability, which foster rapid water uptake and oxygen diffusion. These results are consistent, who reported the same enhancement in water absorption as a result of plasma-induced etching on the surfaces of seeds (Jiang *et al.*, (2014). Furthermore, CP stimulated antioxidant enzymes such as catalase (CAT) and superoxide dismutase (SOD). This response indicates that the reactive oxygen and nitrogen species (RONS) generated during the process produced low-level oxidative stress, priming the internal defense mechanisms of the seed, which is similar to observations (Ling *et al.*, (2014). The SEM analyses confirmed changes in the seeds' structures on the seed coat, while the OES confirmed that the active species in CP were present, which could subsequently lead to the changes in biochemistry and physical structure that we observed.

However, excessive exposure times produced an overload of oxidative capacity and possible damage to the tissues, further demonstrating the need for exact optimization of plasma dose.

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