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Ultrasound Seed Priming: Biophysical Mechanisms And Molecular Pathways For Enhancing Abiotic Stress Tolerance In Crops

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Abstract
Seed priming is a pre-sowing technique that involves controlled hydration of seeds to initiate metabolic processes for germination without radicle protrusion, followed by drying to the original moisture content. This method enhances speed of germination, uniformity, vigor, and tolerance to abiotic and biotic stresses, ultimately improving crop establishment and yield. Ultrasound seed treatment has emerged as a sustainable, chemical-free priming method designed to enhance seed vigor, increase germination rates, and improve resilience to abiotic stresses. This review classifies the types of ultrasound as low-frequency cavitation for modifying seed coats and facilitating better water uptake, high-frequency sonication for stimulating metabolic activities while explaining mechanisms such as acoustic streaming that loosens cell walls, regulation of reactive oxygen species that boost antioxidant defenses, and epigenetic changes that improve stress resistance. These methods consistently enhance germination consistency, expedite seedling emergence, and elevate overall crop performance under adverse conditions, as demonstrated by biophysical seed treatment. Upcoming possibilities integrate ultrasound technology with Artificial Intelligence for forecasting ideal parameters through machine learning using initial data, and the Internet of things for automated, instantaneous distribution in precision agriculture systems, facilitating scalable seed improvement in response to climate fluctuations.

Keywords Ultrasound seed priming; Cavitation; Stress tolerance; Crop improvement; AI integration; IoT precision agriculture.

1. INTRODUCTION

Seed germination is widely recognized as a critical and highly vulnerable stage under abiotic stress because it marks the transition from a dry, dormant seed to a metabolically active seedling, and any disruption in water uptake, temperature, ionic balance, or redox homeostasis can delay, reduce, or completely inhibit radicle emergence and seedling establishment [1]. Abiotic stresses such as drought, salinity, and temperature extremes reduce water availability, alter mobilization of stored reserves, disturb hormonal balance (increasing ABA, reducing GA), and damage proteins and membranes through osmotic, ionic, and oxidative stress, thereby lowering germination percentage, slowing germination, and weakening seedlings [2]. Under drought and salinity, reduced external water potential and toxic ion accumulation create osmotic stress, which perturbs water balance, turgor maintenance and nutrient status, leading to growth inhibition and secondary metabolic disturbances [3]. These ROS-driven injuries are key reasons why abiotic stress reduces photosynthesis, impairs energy production, alters central carbon and amino-acid metabolism, and drives large-scale metabolic reprogramming in primary and secondary metabolites [4].

Conventional seed priming methods such as hydropriming, osmopriming, and halopriming improve germination but it also have limitations linked to both chemicals and performance consistency [5]. Hydropriming, which uses only water, is cheap and eco-friendly, yet water uptake is uncontrolled, leading to unequal seed hydration and non- uniform emergence, and it must be stopped at a precise time to avoid radicle protrusion, making protocols hard to standardize across species and seed lots [6]. Osmopriming and halopriming depend on osmotic solutions or salts (e.g., PEG, NaCl, KNO_3, $CaCl_2$), which can create challenges such as the need for aeration due to high viscosity (PEG) and potential contamination that may require pesticides, introducing concerns about chemical use and residues in the priming medium [7]. All these methods often reduce seed storage life after priming, as primed seeds tend to deteriorate faster during storage, which is a major practical limitation for large-scale seed handling [8].

Ultrasound seed priming is emerging as a green, fast, and residue-free alternative to conventional chemical or solution-based priming, offering improved germination, seedling vigor, and stress tolerance without adding external agrochemicals or leaving persistent residues in plants or the environment [9]. Ultrasound consists of acoustic pressure waves above 20 kHz, and low-frequency, high-intensity waves in the 20–100 kHz range can penetrate seeds and interact with biological tissues through mechanical and mild thermal effects, inducing cavitation, micro-cracks and pores in the seed coat, enhanced water and oxygen uptake, and modulation of cellular metabolism and gene expression [10]. These interactions modify hydration pathway, stimulate enzymes such as amylases and proteases, enhance antioxidant and defense systems, and can reprogram hormonal, lipid, and even epigenetic pathways, thereby promoting germination, vigor, and improved performance under abiotic stresses [10]. The optimal ultrasound parameters like frequency, power, duration of exposure for enhancing germination/seedling effects vary significantly across species (seed) as summarized in table 1.

TABLE 1: Seedling development from seeds of different species stimulated by ultrasound

Species (seed)	**Frequency of ultrasound**	**Power of ultrasound**	**Optimum duration of exposure**	**Sonication temperature**	**Main germination/seedling effects**	**References**
Capparis spinosa (Caper bush)	-	20-100 W in Ultrasonicator probe	60-300 s	53.5°C at 100 W	Maximun germination	[11]
Zea mays (Maize)	20-45 KHz	-	30 min	30°C	Germination, radicle length and hydrolytic enzymes increases, ultrasound induced enhanced respiration, starch, dry matter and GABA.	[12]
Glycine max (Soybean)	20/60 KHz dual	240 W	-	25°C± 3°C	Shortened sprouting duration	[10]
Hordeum vulgare (Barley)	20 KHz in probe ultrasonicator	460 W	5-15 min	30°C	Improved hydration and shell fragmentation that enhances water uptake	[13]
Senna multijuga (Forest legume)	20 KHz in probe ultrasonicator	250, 350, 450 W	5 min	-	Low residue, rapid seedling production	[14]

2. Fundamentals of Ultrasound Technology

2.1. Nature of Ultrasound Waves

Ultrasound is a form of sound energy that uses mechanical waves with frequencies higher than 20 kHz, which is above the range of human hearing [15-17]. These waves need a liquid medium to travel, because their motion is created by vibrating particles transmitting energy from one to another [15]. As ultrasound waves passes through a liquid, it propagates as longitudinal waves, made up of repeating cycles of compression (where molecules are pushed closer together and pressure increases) and rarefaction (where molecules spread apart and pressure decreases), producing alternating high- and low-pressure regions in the fluid [18]. Ultrasonic waves moving through water lead to the phenomenon called cavitation, where micro-bubbles are formed [11]. Ultrasonic treatments are typically administered using either an ultrasonic bath, which provides indirect and uniform cavitation, or a probe sonicator, which delivers high intensity localized energy directly into the medium [14] as given in figure 1.

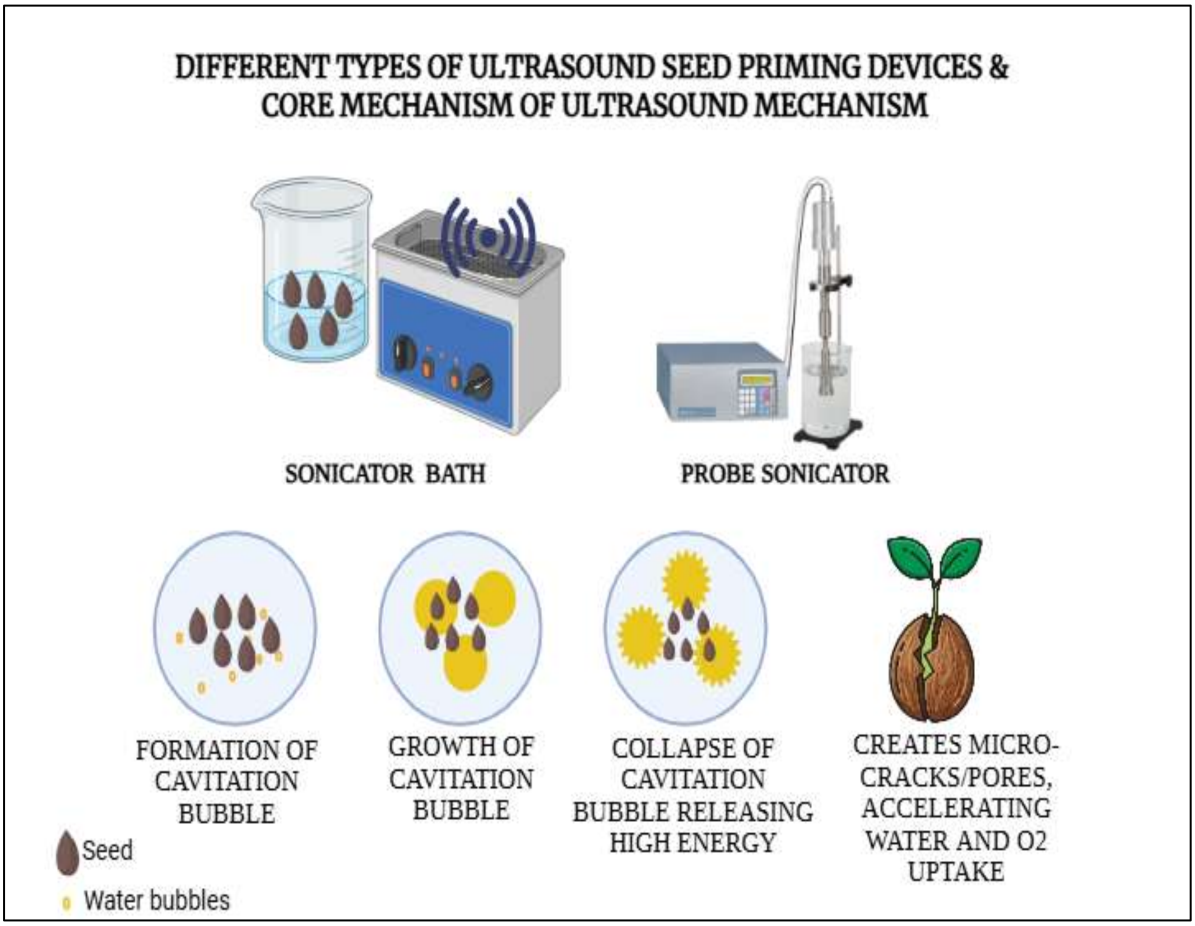

FIGURE 1: Representation of ultrasound seed priming devices and schematic representation of a ultrasound seed treatment mechanism (www.biorender.com)

2.2. Acoustic Cavitation

Under ultrasound, tiny gas or vapor pockets in a liquid can grow into micro-bubbles, then rapidly oscillate and collapse [19]. Their life cycle typically involves nucleation from pre-exist micro-bubbles, rapid expansion driven by pressure or temperature changes, and a violent implosion [20]. During collapse, the bubble's stored potential energy is converted into intense local effects as sharp pressure waves, high-speed micro-jets, and a strong rise in temperature and pressure in a very small region of the fluid, which can alter local flow, enhance mixing and mass transfer, erode nearby surfaces, and even drive thermo-chemical reactions inside the bubble [20-23]. The collapse of cavitation bubbles or the action of shock waves near a solid boundary can produce intense micro-jets and high-pressure shock-waves that strike the nearby surface (seed coat). These micro-jets are thin, fast liquid or material jets formed when a distorted bubble or rough surface feature focuses the flow during collapse, while the associated shock-waves radiate outward as short, high-pressure pulses [24, 25]. Together, they deliver localized, powerful impacts to the surface, concentrating energy in small areas and potentially altering or damaging the outer layers of seed coat [24, 25] as explained in figure 1.

2.3. Types of Cavitation

Cavitation in an acoustic environment is generally classified as stable or transient (inertial), depending on how bubbles travel and collapse [26]. Bubbles in stable cavitation form slowly from gas nuclei and then pulse for many acoustic cycles about an equilibrium size without catastrophic collapse, resulting in oscillations and micro-streaming that can have a gentle effect on tissues [19]. Transient cavitation occurs when a nucleus rapidly expands over one acoustic cycle into a much larger bubble, which then collapses and rebound violently, often fragmenting or disappearing after one or a few cycles; this generates extreme local temperatures and pressures, shock waves, and micro-jets, which drive strong mechanical, chemical, and biological effects such as erosion, free radical formation, and tissue damage [26] as explained in figure 2.

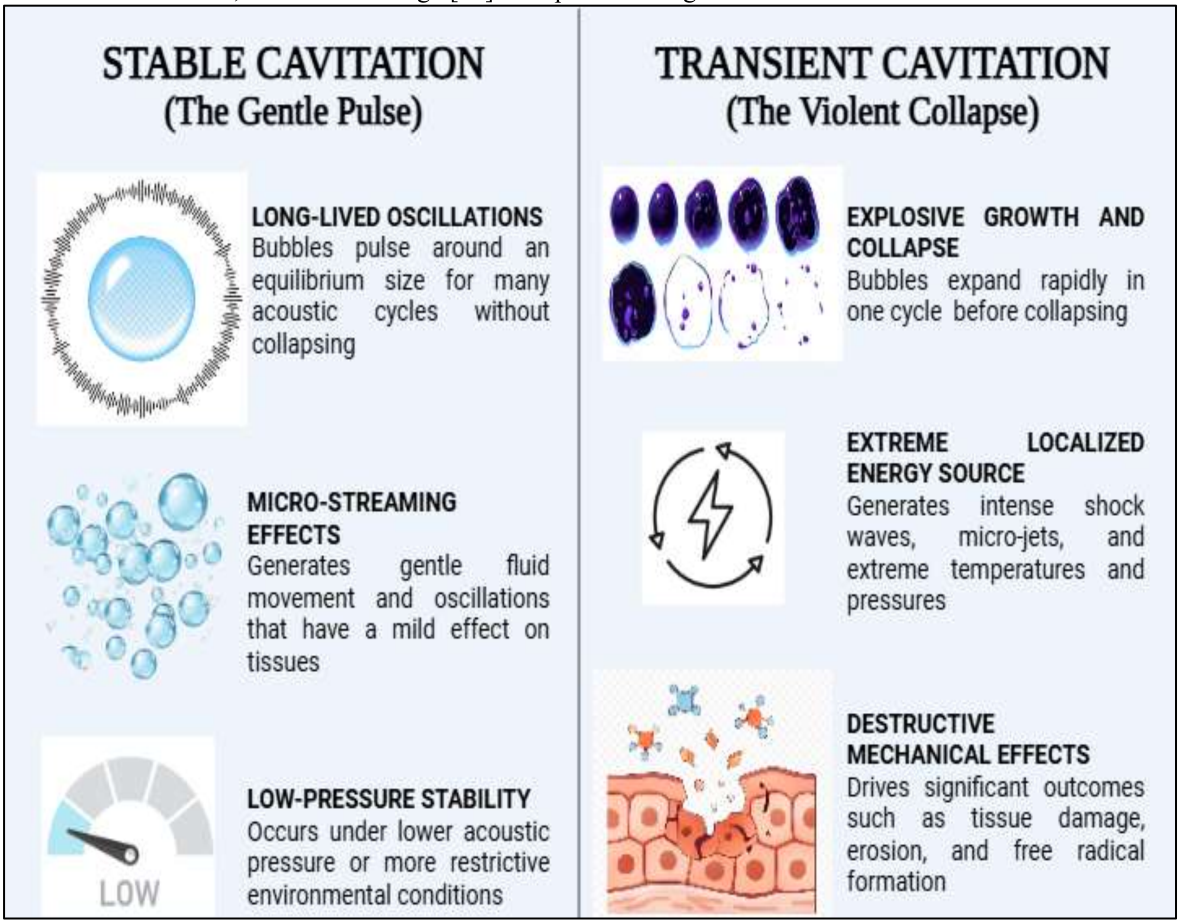

FIGURE 2: Comparative dynamics of stable and transient acoustic cavitation (www.biorender.com)

The stability or instability of a nucleus is determined by factors such as acoustic pressure, frequency, and surrounding material properties. Higher pressures and favorable conditions promote explosive, transient growth and collapse, while lower or more restrictive conditions favor long-lived, oscillating bubbles [26].

2.4. Concept of Ultrasound Seed Priming

Ultrasound seed priming or sono-priming, means treating seeds for a controlled time with ultrasound waves while they are in water [9]. In this method, seeds are immersed in an aqueous medium and exposed to ultrasound waves that creates pressure variations, micro-bubbles, and vibration around and within the seed tissues [11, 27]. This simultaneously provides physical stimulation (via cavitation, microcracks, and "sponge effect" pumping water into the seed) and modifies hydration dynamics by accelerating and increasing water uptake and internal moisture binding [28]. Because ultrasound can disrupt or weaken the seed coat, open micro-cavities, and induce localized mechanical and sonochemical effects in the surrounding liquid, it is considered different from conventional priming [29]. As a result, sonopriming accelerates imbibition and modify metabolic and molecular processes associated with germination, such as enzyme activities, hormone balance, and gene expression, offering a distinct physical, non-chemical priming strategy [9].

2.5. Comparison with Other Priming Methods

Different priming media regulate the rate and depth of seed hydration in distinct ways, but all converge on activating early germination and protective metabolism before radicle emergence, as documented across multiple recent reviews and mechanistic studies given in table 2.

TABLE 2: Overview of major seed priming methods and their scientific basis

Priming methods	Priming medium	Key metabolic/ physiological processes activated	References
Hydro-priming	Soak seeds in water for a particular time specific for crops, then dry back to the original moisture content	Starts normal germination metabolism (protein synthesis, respiration) by raising seed moisture, without radicle emergence	[8]
Halo-priming	Soak in inorganic salt solutions (NaCl, KNO3, CaCl2, etc.)	Lowers water potential with salts, slow water entry; cations (K^+, Ca^{2+}) also act as nutrients/signals	[5]
Osmo-priming	Soak in solutions of PEG, mannitol, sorbitol, glycerol, etc.	Low water potential causes slow, controlled imbibition, activates early germination processes but prevents radicle protrusion; alters seed coat and water channels, improves water uptake and stress tolerance	[5, 8]
Bio- priming	Combine controlled hydration with inoculation by beneficial microbes (bacteria, fungi)	Microbes colonize seed surface, produce hormones and protect from pathogens; improves germination, seedling biomass, ion balance and stress tolerance	[5, 8]
Sono-priming	Ultrasound applied during soaking; ultrasound induced cavitation and pressure cycles boosting hydration rate	Ultrasound plus temperature increases initial water absorption rate; reduces soaking time by ~50% while maintaining high germination, with SEM showing water entry through newly formed micro-cavities	[29]

3. Biophysical Effects of Ultrasound on Seeds

3.1. Seed Coat Modifications

Ultrasound seed priming creates cavitation, wherein collapsing micro bubbles apply mechanical stress to the seed coat, resulting in surface erosion that creates fissures, pores, and micro-cracks, thereby enhancing coat porosity [11, 30]. These structural modifications, frequently focused near the hilum and outer testa, lower resistance to mass transfer and establish new or expanded routes for water and gases [9, 10, 28, 30]. Consequently, the first stage of imbibition is expedited, with sonicated seeds demonstrating quicker and frequently higher water absorption than control seeds [30, 31]. Identical micro-structural changes aid in oxygen absorption, as a more porous and fractured coat enables better air diffusion into the seed, assisting in overcoming the typical barrier of the seed coat and promoting metabolic activation and germination [31, 32].

3.2. Water Uptake Kinetics

Ultrasonication accelerates the imbibition phase of the seeds so they quickly reach the moisture levels needed to start metabolism, shortening the lag phase before visible germination begins and often synchronizing with seed germination [33]. In many species, sonicated seeds absorb water faster and/or at higher levels than controls, reducing hydration or soaking time by approximately 25–54% and shortening the lag phase or germination period by approximately 20–45% [13, 29, 34]. This faster hydration moves seeds sooner from initial rapid imbibition to active metabolic stages, thereby helping radicle emergence occur earlier and more uniformly throughout the seed batch, reflected in higher germination rates, faster average germination time, and improved or more uniform seedling emergence and vigor in crops such as pumpkin, corn, beans, barley, mung bean, pea chickpea, wheat, watermelon and rice [29, 33].

4. Biochemical and Physiological Responses

4.1. Reactive Oxygen Species (ROS) Modulation

Reactive oxygen species (ROS) are highly active oxygen-based molecules, at low to moderate levels, are not only harmful byproducts but also important cellular messengers [35]. Hydrogen peroxide, do not cause damage but act as signaling molecules that coordinate many cellular processes such as growth, proliferation, differentiation, and stress responses [35-38]. This controlled ROS "oxidative eustress" activates redox-sensitive signaling pathways and transcription factors (e.g., Nrf2, NF-κB, MAPK, PI3K/Akt) that regulate genes involved in cell survival, metabolism, and adaptation to changing encironment [35, 36, 39, 40]. As part of this response, cells activate a network of enzymatic and non-enzymatic antioxidant defense mechanisms, such as superoxide dismutase, catalase, peroxidase, glutathione, and other small antioxidant molecules, that collectively scavenge excess ROS, maintain redox balance, and prevent the transition from beneficial signaling to destructive oxidative stress [35, 40-42].

4.2. Antioxidant Enzyme System

The antioxidant enzyme system serves as a crucial mechanism that becomes increasingly active in response to stress in plants [42]. Enzymes such as superoxide dismustase (SOD), catalase (CAT), peroxidase (POD/POX), and ascorbate peroxidase (APX) are frequently upregulated in these stress conditions to manage reactive oxygen species and maintain a stable internal redox environment [43, 44].

In stress conditions like drought, salinity, extreme temperature or pathogen invasion, SOD initially transforms the highly reactive superoxide radical into hydrogen peroxide and oxygen, while CAT, APX and various peroxidases subsequently decompose hydrogen peroxide into water molecules and oxygen, preventing its oxidative damage [43-46]. Elevated activities of SOD, CAT, POD and APX have consistently been linked to improved stress tolerance in crops like soybean, rice, bean and several Arabidopsis ecotypes, where elevated or prolonged enzyme activities correspond with enhanced protection of cellular structures, photosynthesis and sustained growth and yield during stress [43-45, 47]. These enzymes serves as a primary defence that preserves redox homeostasis under stress by effectively surplus ROS while permitting regulated ROS levels to participate in signaling and adaptation [43-45, 48]. Biochemical and physiological responses triggered by Ultrasound seed priming in developing seeds is illusrated in figure 3.

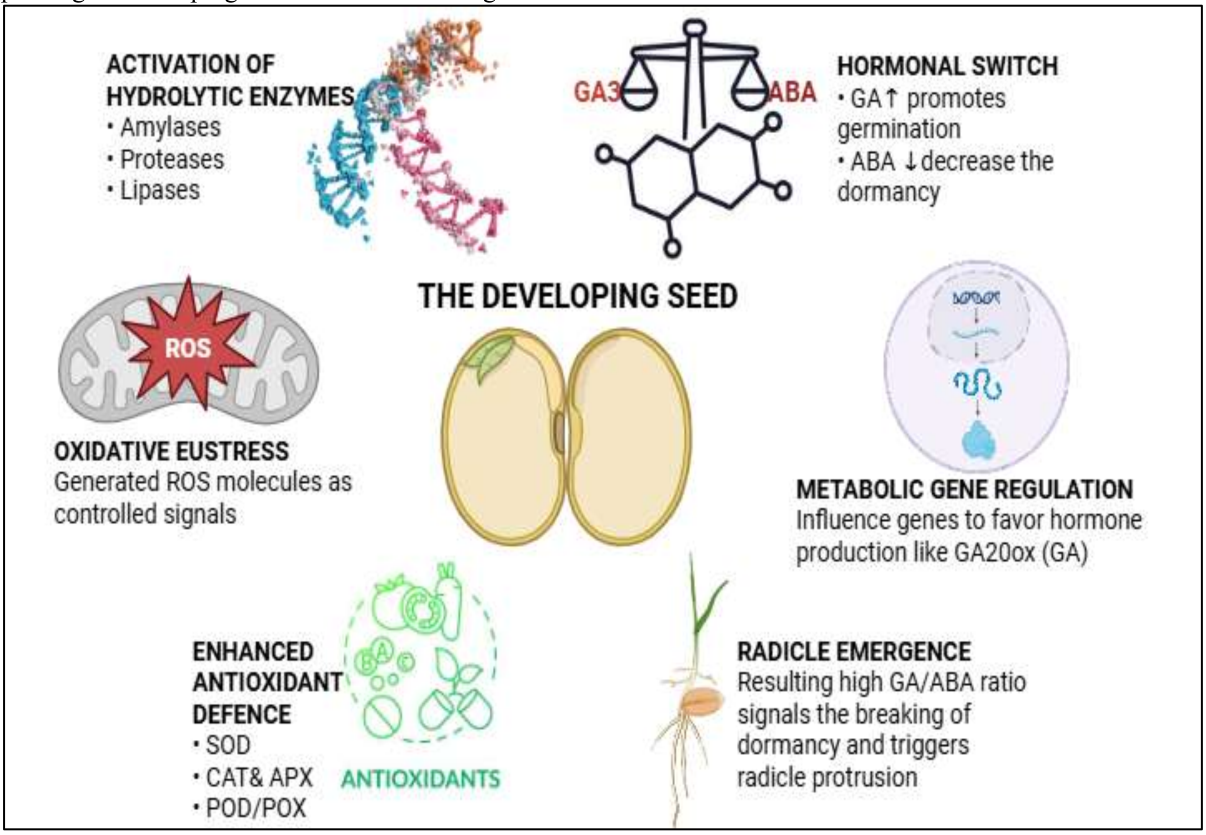

FIGURE 3: Biochemical and physiological responses triggered by Ultrasound seed priming in developing seeds (www.biorender.com)

5. Ultrasound Priming in Abiotic Stress Management

5.1. Drought Stress

Ultrasound seed priming markedly enhances germination and drought resilience across crops like wheat, maize, and Senna [12]. In case of drought stress, priming treatments assist plants in utilizing water more effectively, regulating their internal water balance, and maintaining growth [49]. Seed priming significantly boost water use efficiency in crops such as soybean and wheat, frequently by decreasing transpiration and stomatal conductance while preserving adequate photosynthesis, resulting in higher biomass or yield [50]. Priming process improve osmotic adjustment by accumulating compatible solutes like sugars, amino acids, proline and glycine betaine, which decrease osmotic potential, enhance cell water status, and safeguard membranes against dehydration [51]. These modifications are strong associated with enhanced root characteristics priming or drought exposure frequently increases the root to shoot ratio, root length, and root volume [49, 51].

Exposure at 65 W for 15 minutes in wheat boosts relative water content, protein levels, SOD and amylase activities, while reducing MDA and electrical conductivity for healthier membranes [52]. In drought-simulated conditions with PEG, ultrasound improves water absorption, reserve utilization, and seedling vigor, countering growth inhibition [53].

5.2. Salinity Stress

Ultrasound seed priming as a physical techniques proved the effectiveness in alleviating salinity stress in plants by decreasing sodium (Na+) toxicity, enhancing the potassium/sodium (K+/Na+) ratio, and improving ion homeostasis and membrane stability [54]. These priming techniques promote the selective absorption of K+ while restricting Na+, by activating ion transporters such as NHX and SOS1, which assist in the elimination of surplus Na+ [55]. Moreover, primed seeds demonstrate enhanced antioxidant enzyme activities and increased osmolyte accumulation which further strengthen cellular membranes and protect against oxidative damage caused by salt stress [56]. The gene expression associated with aquaporins and stress signaling pathways also enhances water absorption, metabolic activity and overall seedling health in saline environment in ultrasound seed priming [28]. And also enhance strong germination, growth and agricultural productivity in saline affected environment [12].

In beans, 20 min of 50 Hz ultrasound significantly raised germination rates and seedling development under mild to moderate salt stress (5–10 dS m^{-1}), increasing the salinity tolerance index by ~38% compared with untreated seeds [57]. In fenugreek, 20 min treatment at 40 kHz improved germination percentage, biomass, plumule/radicle lengths, and vigor index under NaCl stress (0–5000 mg/L)- despite salinity reducing germination by up to 74% and elevating osmoregulators (soluble proteins, carbohydrates, proline)- with RAPD-PCR confirming 49.72% DNA polymorphism from treatment-induced changes [54].

5.3. Heavy metal stress

Ultrasound-assisted seed treatment helps reduce heavy metal stress by decreasing the toxic metals and enhancing antioxidant-driven detoxification mechanisms in plants. When rice was grown in soils contaminated with lead (Pb), ultrasonic seed treatment lowered Pb levels in roots, stems, leaves, panicles, and particularly in brown rice, thereby reducing the amount of this toxic metal that entered the edible grain [58]. Meanwhile, plants treated with ultrasound exhibited elevated levels of crucial antioxidant enzymesincluding superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) along with higher concentrations of proline and soluble proteins, and lower levels of malondialdehyde (MDA), suggesting enhanced removal of reactive oxygen species and better membrane protection under lead stress [58]. In wheat seedlings subsequently exposed to cadmium and lead, prior ultrasonic treatment similarly boosted the activities of catalase, superoxide dismutase, and glutathione reductase, while reducing levels of malondialdehyde, superoxide, and electrolyte leakageindicating enhanced antioxidant defense and better membrane integrity under heavy metal stress [59].

This priming improved cadmium detoxification and physiological-biochemical status in sugarcane [60], lowered lead absorption while raising proline (89%), soluble proteins, and enzymes and reducing MDA (67%) in rice for better yield [58], accelerated germination, chlorophyll/protein synthesis, and biomass in wheat under Cd/Pb stress [59], and strengthened defenses, lowered MDA/Cd accumulation, and increased seed yield by 11–16% in rapeseed grown on contaminated soil. The integrated role of ultrasound sonication in alleviating abiotic stress through physiological, biochemical, and molecular regulation is summarized in figure 4.

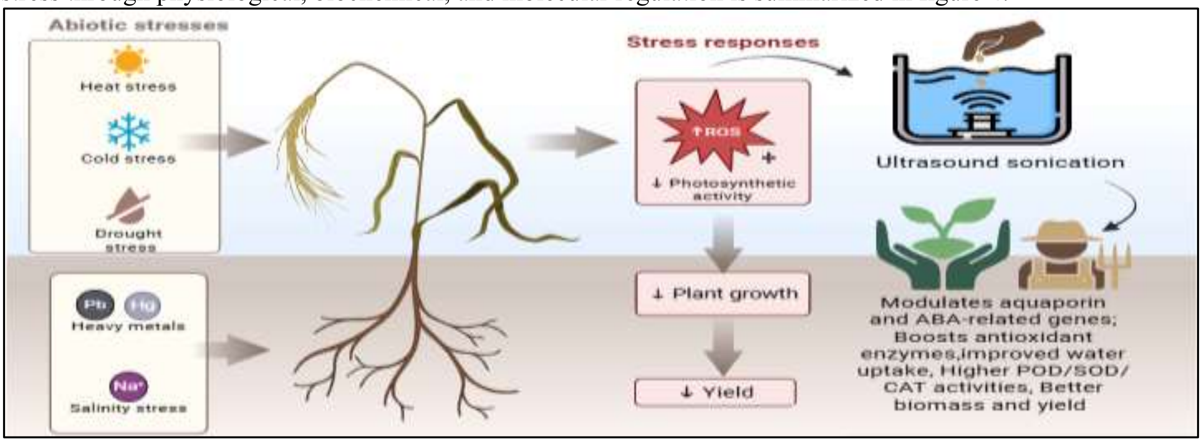

FIGURE 4: Schematic representation of advantages of ultrasound seed priming treatment in abiotic stresses (www.biorender.com)

6. Advantages of Ultrasound Seed Priming

Ultrasound seed priming is a chemical free, pre-sowing treatment, physical method, where seeds are treated with acoustic waves in water or any other medium offering an environmentally friendly comparing to the conventional chemical priming, which leave harmful residues and cause agricultural pollution. Ultrasound promotes germination and early seedling growth by increasing the absorption of water and oxygen and boost seed metabolism, notably through enhanced starch breakdown via the activation of enzymes like amylases and other hydrolases [10].

Ultrasound induced cavitation and mechanical vibration create micro-cracks and pores in the seed coat, enhancing permeability and accelerating uniform hydration and germination, typically reducing germination time by 30-45% and boosting the final germination rate [10, 28]. On a molecular level, ultrasound can enhance the expression of aquaporin genes, suppress genes involved in abscisic acid biosynthesis, and influence antioxidant and metabolic enzymes, thereby promoting robust and synchronized seedling development even in sub-optimal soil environment [28, 55].

Ultrasound devices have already been evaluated across various crops including maize, tomato, turnip, beans, rice, and barley showing consistent enhancements in germination, seedling strength, biomass and in certain instances, yield and quality [28]. This indicates that ultrasound is fast, uniform, and technically scalable for industrial seed treatment, while also supporting sustainable, low-chemical farming practices [9, 28].

7. Disadvantages of Ultrasound Seed Priming

Non-chemical seed treatment like ultrasound and various physical technologies enhance germination; however, their broader implementation is limited by significant scientific and practical challenges . With high treatment intensities, direct contact with strong electric field, frequency, reactive species, UV light, or oxidative agents harm the seed coat and compromise viability of the seeds [10].

The majority of demonstrations a still lack the field scale validation concerning long term yield, economic advantages, and performance across diverse farm environments. Moreover, physical technologies (such as ultrasound, cold plasma, etc.) necessitate specialized high voltage or gas-handling apparatus, which can be energy consuming, expensive, and technically challenging. Although ultrasound seed priming is eco-friendly, the equipment needed is expensive and specialized, it is described as a capital-intensive technique requiring skilled personnel to operate the instruments compared to traditional, low-cost priming methods [13].

8. Research Gaps and Future Perspectives

Research on seed priming increasingly emphasizes key gaps and future directions that are particularly significant for ultrasound and various physical and nano-enabled therapies. Recent studies highlights the advantageous of exposure but fail to provide strong dose-response and frequency optimization models that formally connect treatment parameters to germination, vigor, and stress tolerance across different genotypes and environments [9]. Additionally, there is a difficulty in coupling multi-omics tools (transcriptomics, proteomics, metabolomics and epigenomics) to unravel the molecular processes of physical seed priming. Seed longevity and post priming storage has significant challenges that advantages can be counterbalanced by decreased storability, urging the development of mechanistically informed priming methods and storage systems to prolong seed viability and innovate longevity improving technologies based on seed aging biology. Need for the development consist of portable, inexpensive, and battery operated ultrasound sensors for field uses like estimating soil porosity, measuring canopy height, and directly evaluating plant water status and frequently combined with Artificial Intelligence (AI) and internet of Thing (IoT) systems for improved data analysis and decision making support [9].

9. Conclusion

Ultrasound seed treatment is leading the way in seed science innovation, with recent advancements from cavitation based priming to frequency-modulated sonication, while revealing complex mechanisms such as improved cell wall permeability, modulation of reactive oxygen species (ROS), and the up-regulation of genes that enhance stress tolerance. These advancements pave the way for revolutionary uses in crop enhancement, improving germination rates, vigor, and resilience against abiotic stresses especially drought in rain-fed systems. As precision agriculture progresses, ultrasound treatments offer sustainable and cost effective methods to strengthen food security in the face of climate challenges, making it essential to pursue further validation and commercialization on a field scale.

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Author Contributions
Subathra G Conceptualization of the study. Manonmani V, Djanaguiraman M Literature collection and analysis. Subathra G writing of original draft preparation. Kavitha S, Vellaikumar S, Suriyaprakash P V review and editing. Lakshmi S, Suriyaprakash P V Figure and table preparation and review. Kavitha S, Suriyaprakash P V Supervision of the review article.
All authors have read and approved the final manuscript.

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Data Availability
No datasets were generated or analysed during the current study. All information discussed in this review article is derived from previously published studies, which have been appropriately cited.

Declarations

Ethical Approval All authors approve ethical responsibilities related to this manuscript.
Consent to Participate All authors give their consent to participate.
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