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Seed priming: an emerging tool towards sustainable agriculture

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ABSTRACT

Agriculture is a vital sector in India, supporting over 80% of the rural population through farming and related activities. To meet the food demands of the country's growing population, it is essential to achieve optimal crop yields. However, challenges such as urbanisation, environmental pollution, biotic and abiotic stresses, and micronutrient deficiencies adversely affect seed germination and crop productivity. This review addresses the various factors hindering seed germination and plant growth, with a particular focus on seed priming techniques and mechanisms. Seed priming enhances the uniformity and vigour of germination, thereby improving crop establishment and yield. The technique activates key metabolic processes that prevent seed deterioration, break dormancy, and induce systemic resistance to stresses. Physiological and biochemical changes induced by seed priming are thoroughly examined. Numerous priming approaches—including hydropriming, halopriming, osmo priming, hormone priming, nutripriming, biopriming, and nano priming have been extensively investigated. Additionally, emerging research on bio-nano seed priming, which integrates nano fertilisers with plant growth-promoting rhizobacteria, presents a novel avenue to further enhance crop productivity.

Keywords: *Abiotic stress, micronutrient, seed germination, urbanisation, dormancy, induce systemic resistance, pollution, uniformity, priming.*

INTRODUCTION

Efficient crop production depends on successful plant stand establishment and high seedling vigour. These factors play a crucial role in determining uniform growth, maturity, and high crop productivity [1]. Environmental pollution and abiotic stresses are major global concerns that significantly affect seed germination, seedling vigour, and ultimately crop yield. These adverse conditions particularly impact agricultural regions characterised by arid and semi-arid climates. Abiotic stresses delay the onset of germination and reduce the growth rate of seedlings, thereby hindering overall plant development [2] [3].
Additionally, these stresses negatively affect soil microbial communities, leading to economic losses in agriculture. As agriculture forms the backbone of India's economy, there is a pressing need for simple, cost-effective, and manageable technologies to enhance crop establishment under diverse environmental conditions. Among the various available approaches, seed priming is an effective and practical technique to synchronise seed germination, improve seedling emergence, and increase crop establishment in the field. Seed priming is an essential tool for enhancing field emergence and crop stand establishment, which ultimately leads to higher productivity [4]. Primed seeds are known to emerge faster, grow more vigorously, and result in higher yields, which is especially important in unfavourable environmental conditions such as drought. This technique also offers the potential to reduce excessive fertiliser usage, boost crop yields through uniform germination, and promote systemic resistance in plants [5] [6].

SEED PRIMING

Seed priming is an innovative, sustainable seed technology to increase seed vigour and crop production without harming the ecosystem [7]. It is a pre-sowing treatment that involves controlled hydration of seeds to activate the initial stages of germination-related metabolism, while preventing the emergence of the radicle (root tip) [8] [9] [10]. This process typically includes soaking seeds in water or various solutions comprising organic or inorganic compounds under controlled environmental conditions, followed by re-drying to their original moisture content before planting. The goal is to initiate biochemical and physiological processes that enhance seed performance, without allowing visible germination to occur. Priming has been shown to improve the rate and uniformity of germination in several seed types, particularly those of vegetables, small-seeded grasses, and ornamental plants. It is also effective in reversing some of the negative effects associated with seed ageing and deterioration. Due to its simplicity, low cost, and minimal risk, seed priming is considered an accessible and efficient technique for improving crop establishment [11] [5] [12] [13].

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The benefits of seed priming are numerous. It promotes rapid and uniform germination, supports seedling emergence across a broader range of temperatures, and enhances early plant development. Additionally, primed seeds often exhibit improved water-use efficiency, deeper root growth, and enhanced metabolic activity, which can help break dormancy and accelerate the development of reproductive structures. Seed priming also contributes to early flowering and maturity, better competition with weeds, and increased resilience to abiotic stresses such as drought and salinity. Furthermore, primed seeds may show greater resistance to soil-borne pathogens, including *Rhizoctonia solani*, *Fusarium* spp., and *Sclerotium rolfsii* [4] [14] [15] [16] [17].

Mechanism of priming

Seed germination is a complex physiological and biochemical process that transforms a quiescent seed into an actively growing seedling. It involves a series of metabolic events that convert stored food reserves into usable energy and structural components, leading to the emergence of the radicle and plumule.

Typically, water uptake during seed germination follows a triphasic pattern:

Phase I – Imbibition:

This initial stage involves rapid water absorption driven by the seed's dry matrix potential. It triggers the reactivation of cellular metabolism, repair of damaged DNA, and restoration of mitochondrial function, which is essential for initiating energy production [18].

Phase II – Lag Phase (Activation Phase):

During this stage, water uptake slows considerably, resulting in only a slight increase in seed fresh weight. This phase is also called the Activation phase, as this period is highly active physiologically and metabolically. Mitochondrial maturation occurs, enabling ATP synthesis; transcription and translation processes resume, and stored macromolecules are mobilised to provide the necessary substrates for growth [6].

Phase III – Germination Proper:

In this final phase, rapid water uptake resumes, leading to radicle protrusion and visible germination. Seedling growth initiates, marking the completion of germination.

In the context of seed priming, seeds are allowed to undergo Phases I and II under controlled conditions but are prevented from entering Phase III by re-drying them before radicle emergence. This controlled pre-germination treatment allows seeds to complete preparatory metabolic steps in advance. As a result, when primed seeds are sown and rehydrated, they rapidly resume germination due to the reduced need for early-stage metabolic activation [19] [20].

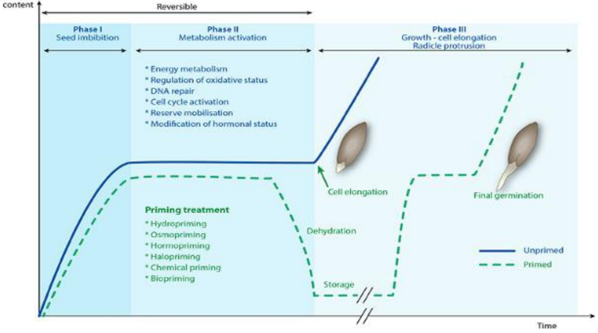

Figure 1: Time of seed imbibition or of priming

The extension of the lag phase during priming enables the synthesis of new mRNA and proteins, enhances the activity of nucleic acid-related enzymes, and increases the total RNA and protein content in seeds. Additionally, it facilitates the repair of membranes damaged during storage or desiccation, thereby improving seed viability and vigour. Overall, priming leads to synchronised radicle emergence, faster germination, and improved seedling establishment.

Physiological and Biochemical Changes

Seed priming induces a range of physiological and biochemical modifications that significantly enhance germination and early seedling development. One of the key outcomes of priming is the synchronisation of germination following dormancy release. It reduces the lag phase during water uptake (imbibition), facilitates the breakdown or neutralisation of germination inhibitors, activates crucial metabolic enzymes, mobilises stored nutrients, and promotes embryonic growth [21] [22]. This includes:

Seed Ultra-Structure

The ability of seeds to germinate seems to be critically determined by a change in the balance between the growth potential of the embryo and the mechanical resistance of the surrounding tissues. In many species, the endosperm tissue enclosing the embryo restrains the germination process acting as a physical barrier, that restricts radicle emergence. Weakening of tissues surrounding the elongating radicle by cell separation due, for instance, to the activity of cell wall hydrolases may occur as a consequence of priming. It induced hydrolysis of the endosperm and increased the endo-β-mannanase activity in the endosperm cap and decreased its mechanical restraint on the elongating embryo. A strong correlation was observed between the lowering of the mechanical restraint and the activity of endo-β-mannanase. Penetration of the structures surrounding the embryo is a consequence of radicle cells' elongation. As XTHs have the ability to cleave xyloglucans and rejoin the cut ends with new partners, they are engaged in cell wall loosening during growth and in the restructuring of the cell walls after extension [23] [24].

Cytoskeleton

Cytoskeleton reorganisation is also necessary to achieve large rates of cells elongation that precedes radicle protrusion. The component of microtubules (β-tubulin) accumulated in seeds during germination and priming, and the expression preceded visible germination. The up-regulation of genes encoding γ- and β-tubulins was also noticed during post-priming germination. In the endosperm, the catabolic changes were limited to the micropylar area, where extensive breakdown of storage cell walls, and partial degradation of protein bodies occurred. During seed germination, storage proteins, which provide a source of reduced nitrogen, and inorganic minerals need to be mobilised to support seedling growth [25].

In addition, a lytic aqueous vacuolar compartment, building up the turgescence necessary for cell expansion and to promote radicle protrusion and embryo elongation, has to be formed. The first one corresponds to globoids specialised in mineral storage and the second one is at the origin of the central lytic vacuole in these cells.

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A major biochemical change involves:

Reverse mobilisation

The metabolism of starch is a vital process influencing seedling vigour, particularly under stress conditions. Enzymes such as α-amylases play a central role by hydrolysing starch into simpler, metabolically usable sugars, thereby supplying energy for embryo development. Seed priming has been shown to enhance the activity of α-amylase and dehydrogenase enzymes, contributing to improved starch degradation, higher ATP production, and elevated respiration rates. Additionally, increased activities of enzymes such as phytase, amylase, and protease have been reported following priming. Priming also helps in the activation of enzymes such as malate synthase and isocitrate lyase, which facilitate the conversion of lipids into carbohydrates [26].

Seed water content

Aquaporins (AQPs) are transmembrane proteins, members of the major intrinsic protein (MIP) family that facilitate rapid and passive water transport across cell membranes and play a crucial role in plant water relations. Plant aquaporins are remarkably diverse with several subfamilies of MIPs identified in dicots and monocots. Among them, the plasma membrane intrinsic proteins (PIPs) and the tonoplast intrinsic proteins (TIPs) subfamilies constitute the largest number of AQPs and correspond to AQPs that are abundantly expressed in the plasma and vacuolar membranes, respectively [27]. Both PIP and TIP subfamilies are believed to play a key role in transcellular and intracellular plant water transport. Accumulation of osmolytes is a crucial mechanism of plant stress tolerance, which reduces the osmotic potential (OP) of cell and allows osmotic adjustment (OA) under adverse environmental conditions. Dehydrins (Late Embryogenesis Abundant Proteins) (group 2 LEA protein) are associated with enhanced stress tolerance in primed seeds. The expression of LEA proteins undergoes sequential changes with a decline during the imbibition phase, upregulation in the dehydration phase, followed by degradation during germination [28] [29] [30] [31].

Cell cycle regulation

Priming induced improvement based on its effect on DNA in relation to activation of DNA repair mechanisms, synchronisation of the cell cycle in G2 and preparation for cell division. During seed maturation, most of the embryo cells are stopped at the G1 or G0 phase of cell cycle, and only some species have a small proportion of cells in the G2 phase. During seed imbibition, meristematic activity is limited; however, some preparation to cell division occurs. Priming increased the ratio of cells in G2 phase to G1 phase and indicates that the beneficial effects of priming on seedling performance are associated with the replicative DNA synthesis prior to germination. This is accompanied by an increase in α- and δ-like DNA polymerase activities in primed seeds and during germination. The initiation of the cell cycle and progression of the cell to S phase may also depend on a G1 checkpoint control [32].

Regulation of oxidative stress

In primed seedlings, different antioxidants such as POD, APX, SOD, and CAT have been known to play an important role in enhancing stress tolerance. These antioxidants may guard the cellular membranes against the harmful effects of ROS, such as H_2O_2, hydroxyl radicals, superoxide radicals, and singlet oxygen.

Enhanced activities of CAT, SOD, and POD in seedlings that emerged from primed seeds have been reported under normal and stress conditions. Plant antioxidant systems scavenge the excessive ROS production induced by various stresses and play an important role during seed storage, germination, and development.

The antioxidant system constitutes both enzymatic (such as APX, CAT, and SOD) and nonenzymatic compounds (e.g., GSH and AsA). Each antioxidant usually has a specific function; for instance, CAT degrades the H_2O_2 into water and oxygen, while APX-induced catalysis of H_2O_2 is reliant on the AsA-GSH cycle. Here, AsA acts as an election donor to stimulate H_2O_2 degradation by the APX, while GSH and its enzymes (monodehydroascorbate reductase; MDHAR, GR, dehydroascorbate reductase; DHAR) are accountable for AsA regeneration. Moreover, various antioxidants can have different functions at a similar developmental phase. For instance, CAT was regulated in dormant mature as well as germinating seeds, whereas APX was not noticed in physiologically quiescent seeds. Seed priming modifies the ROS accumulation and alters the expression of genes and enzymes of the antioxidative defence system [33] [34].

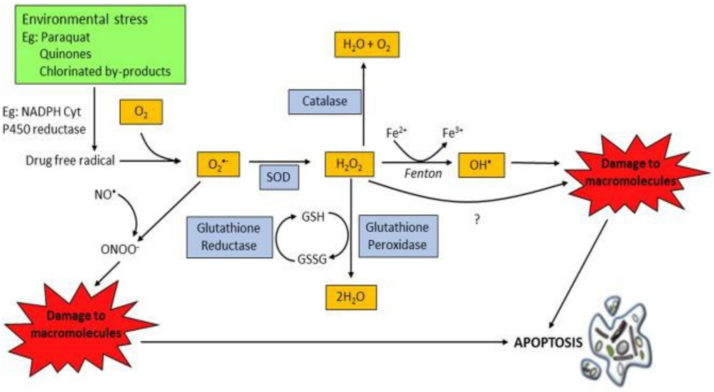

Figure 2: Regulation of oxidative stress

Enzyme balance

Increased level of Gibberellic Acid. Two different mechanisms are suggested regarding the role of ethylene in seed priming: (1) Higher ethylene production enhances the activity of endo-β mannanase, which can help germination at high temperature via weakening of endosperm, (2) Ethylene can regulate the osmotic adjustment in primed seeds and increase germination even under stressful conditions [34].

TECHNIQUES OF PRIMING

Nowadays A variety of seed priming techniques have been developed to enhance seed quality and improve germination performance. Common methods include hydropriming (soaking seeds in water), halopriming (using salt solutions), osmopriming (using osmotic solutions such as polyethene glycol), matrix priming (imbibing seeds in solid matrices),

Other advanced techniques involve the use of bioactive compounds or materials. These include hormonal or growth regulator priming, micronutrient-based seed treatments (also referred to as *nutripriming*), and biopriming, where seeds are inoculated with beneficial microorganisms such as *Pseudomonas aureofaciens* or species of *Trichoderma*. Furthermore, nanopriming- coating or treating seeds with nanoparticles—has emerged as a novel strategy for improving germination and stress resistance [35].

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It is important to note that each crop species—and often each cultivar—may respond differently to priming. Therefore, selecting the appropriate priming method requires careful optimisation of key factors such as the duration of treatment, type and concentration of priming agents, seed physiological status, and storage conditions (e.g., moisture levels, temperature, and oxygen availability). These parameters are typically refined through empirical testing and experimentation for each specific crop variety [19].

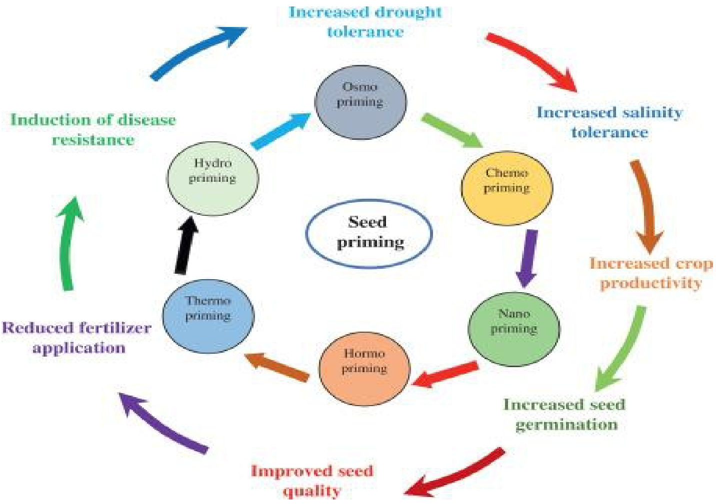

Figure 3: Different methods of priming

1. Hydro-priming

Hydro-priming is an inexpensive, low-risk technique in which seeds are soaked in distilled water at an appropriate temperature for a specific period of time and then dried again to approximate their original moisture content before sowing. No use of additional chemical substances as a priming agent makes this method a low-cost and environmentally friendly method. This leads to an increase in process of germination, accelerates seedling growth and strength [36]. This priming method is particularly useful in regions with unfavourable climatic conditions such as high temperatures and water stress, as it increases the efficiency of water uptake and seed hydration [37]. Hydro-priming has demonstrated a multitude of advantageous effects on crop production. It also increased germination percentage and seedling emergence, which cause productive use of resources (soil, light) to increase the amount of grains. A decrease in seed vigour is an indication of electrolyte leaching due to an increase in membrane permeability. Electrolytes such as inorganic ions, amino acids and sugars are leached, which have high impact on metabolism and different activities involved in synthesis, causing a decrease in germination and overall growth of the seedling. Priming seeds might have repaired seeds by reducing electrolyte leakage, repair of biomolecules such as DNA, RNA, proteins, enzymes and membranes. Hydro primed seeds showed maximum results, suggesting that ion accumulation in the seed has no toxic effect on the embryo. This treatment thus can be used to increase tolerance in drought conditions and enhance growth leading to an environment-friendly technique for improving crop yield [14].

2. Halo-priming

Halo-priming is a technique which involves submerging seeds in solutions of inorganic salts, viz., sodium chloride, potassium chloride, potassium nitrate, calcium chloride, etc. This pre-treatment of seeds with inorganic substances has been found to enhance crop growth and resistance to diverse abiotic stressors, ultimately leading to ameliorated germination, establishment, and yield of crops grown in saline soils [38] [39].

3. Osmo-priming

Osmo-priming involves soaking seeds in an osmotic solution with low water potential instead of pure water. Due to low water potential of osmotic solutions, water enters the seed slowly, which allows gradual seed imbibition and activation of early phases of germination but prevents radicle protrusion followed by air drying before sowing. Various osmotic priming agents such as sugar, polyethene glycol (PEG), glycerol, mannitol, sorbitol and specialised vermiculite compounds are used, of which PEG is mostly preferred [40].

4. Hormonal priming

Hormonal priming refers to seeds in the presence of plant growth regulators, which can have a direct impact on seed metabolism. The following regulators are commonly used for hormopriming: abscisic acid, auxins, gibberellins, kinetin, ethylene, polyamines, and salicylic acid (SA), Gibberellic acid (GA_3) and PEG priming improved photosynthetic properties, antioxidant system, seedling emergence, and growth of white clover on heavy metal polluted soil. Biochemical (protein content, carbonic anhydrase (CA) activity) and growth parameters (seed yield and leaf area/plant, pod number and shoot length) were also enhanced [41] [42] [43] [44].

Gibberellins are known to regulate developmental and physiological processes such as germination, stem, leaf growth, synthesis of food, transporting and partitioning it, and stimulating transcription of hydrolytic enzymes mRNA in various plants. CA enhances membrane permeability and nutrient absorption.

5. Solid Matrix priming

Solid matrix priming is a seed priming technique that involves mixing seeds with water and solid materials at specific proportions [45]. Common solid carriers in this method include vermiculite, charcoal, clay, and sand. In solid matrix priming, the seeds are mixed with a medium that slowly wets them, making them ready for germination. Solid matrix priming has been found to be an effective method for improving seed vigour and germination in various crops. For instance, solid matrix priming of maize seeds using sand was shown to increase α-amylase activity, membrane system integrity, and speed of emergence [46]. Studies have also demonstrated the effectiveness of solid matrix priming using other materials.

6. Nutripriming

Nutri-priming is a pre-sowing seed treatment technique that involves soaking seeds in a nutrient solution to improve their quality and enhance their nutrient content. Micronutrients are important for plant growth as they carry out two vital processes in plants, namely photosynthesis and respiration whose limitation can decrease the overall growth and grain yield [47]. To overcome this problem, micronutrients can be used in three ways, such as applying them to the soil, spraying them on leaves/plant or directly applying them to seeds. Amongst them, seed treatment has been proved better option to improve seedling growth and grain yield as less micronutrient will be needed. Numerous studies have investigated the effects of nutri-priming on different crops, with promising results.

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These findings demonstrate the potential benefits of nutri-priming for crop production, highlighting the importance of nutrient uptake and the potential for enhancing crop yield and quality. The reviews suggest that nutri-priming can be an effective seed pre-treatment technique for enhancing seedling growth and improving crop yield, particularly under stress conditions. However, the optimal duration and concentration of nutrient solution may vary depending on the crop and growing conditions, and careful attention should be paid to avoid over-soaking and nutrient toxicity [48].

7. Bio-priming

Bio-priming involves the treatment of seeds with beneficial micro-organisms. Micro-organisms which protect plants from pathogens and improve their growth are used. Such seed treatments promote germination through environmental signals, mRNA activation/ depression, membrane permeability and effect on pathogens [49].

This plant growth-promoting rhizobacteria show beneficial effects as they have the potential to produce growth hormones (GA_3, IAA), help in nitrogen fixation, produce antibiotic enzymes against pathogens, solubilise minerals and help in their absorption by roots [50] [51] [52].

8. Nano priming

Nano priming is a modern seed treatment technique that uses nanoparticles such as zinc oxide, iron oxide, titanium dioxide, silver nanoparticles, etc. to improve seed germination and plant growth. These tiny particles can carry nutrients, fertilisers, or protective chemicals and deliver them directly to the seed in a slow and controlled way. In this priming, seeds are soaked or coated with nanoparticle-based solutions. These nanoparticles are small enough to penetrate the seed coat and interact with internal tissues. Their high surface area, reactivity, and controlled-release properties enable them to enhance water uptake and metabolic activity, activate seed enzymes critical for germination. Improve nutrient availability and uptake. Induce tolerance against abiotic and biotic stresses. The interaction between nanoparticles and seed tissues can also trigger antioxidant defence mechanisms, enhancing the seed's ability to cope with oxidative stress caused by drought, salinity, or temperature extremes [53] [54].

This helps the seed grow better, even under poor soil or environmental conditions. One of the main benefits of nano priming is that it allows for targeted delivery, meaning the right amount of nutrients goes exactly where it's needed. This reduces waste and lowers the need for excess fertilisers or chemicals. Nano priming can also improve the seed's resistance to stress, such as drought or disease. Because of its precision and efficiency, nano priming is becoming an important tool in agriculture to increase crop yields and make farming more sustainable [55].

The effect of silver nanoparticles (Ag NPs) on chilli seeds was an increase in per cent germination, seedling growth, shoot length, and chlorophyll content, whereas a decrease in root length was observed at higher concentrations. Enhanced biochemical parameters may be the effect of the translation process, increasing protein level, improved electron transport, photosynthetic efficiency and ribulose-1, 5-bisphosphate carboxylase/oxygenase activity leading to carbohydrate synthesis, and electron transport chain leading to increased pigments and chlorophyll content. This may have led to enhanced. Hence, the dose of nanoparticles needs to be standardised for each crop [56].

Nano priming is a promising technology that combines the benefits of seed priming with nanotechnology to improve seed performance, enhance germination, promote early growth, and increase resistance to stress and disease. While challenges remain, especially regarding safety and standardisation, it offers a smart and sustainable path forward for modern agriculture. Despite its potential, nano priming presents certain challenges [57]:

- **Toxicological Concerns**: Excessive or inappropriate use of nanoparticles may harm plant tissues, beneficial soil microorganisms, or accumulate in the environment.
- **Lack of Standardisation**: Optimal concentrations, exposure durations, and particle sizes must be tailored to specific crops and conditions.
- **Cost and Accessibility**: Some nanoparticle formulations are expensive or require specialised equipment for application.
- **Regulatory and Environmental Impact**: Long-term ecological effects and biosafety regulations remain under investigation.

CONCLUSION

Seed priming is a useful method that shown significant potential in improving germination, encouraging early flowering and maturation, breaking seed dormancy, and enhancing plant resistance to various abiotic stresses and soil-borne diseases through the activation of systemic resistance mechanisms. So, seed priming can be considered as a better solution against problems related to germination when seeds are grown under unfavourable conditions. Research across different crops has demonstrated the effectiveness of various seed priming methods in boosting crop yield, particularly under less-than-ideal growing conditions. While each priming technique contributes positively to plant growth and productivity, standardisation is necessary due to the influence of multiple interacting factors.

FUTURE SCOPE

Among all methods of seed priming, biopriming with plant growth-promoting rhizobacteria (PGPRs) has been especially promising not only for enhancing plant development but also for rejuvenating the soil microbial community. Additionally, nano-priming is attracting interest for its ability to deliver nutrients or agrochemicals in a targeted and controlled manner. Therefore, integrating fertilisers with PGPRs referred to as bio-nano seed priming-holds great promise for improving agricultural productivity in the future.

CONFLICT OF INTEREST

The authors declare that there is no conflict of interest regarding the publication of this manuscript.

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