

Review Article

Review of Drought Stress and Seed Priming Effects on Upland Rice Yield and Longevity

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Abstract

Unequal plant stand and poor germination are major constraints in seeds under areas which receive erratic and low rainfall. Seed priming has emerged as a crucial strategy to enhance the biochemical, physiological, and ecological resilience of seeds and seedlings. Employing suitable priming methods at different developmental stages can significantly improve drought tolerance in plants. Research indicates that the primary factors leading to seed deterioration are the combined effects of low temperatures and moisture levels, which trigger abnormal biochemical and physiological responses. Seed priming techniques show promise due to their simplicity and adaptability in local agricultural practices. However, one of the challenges associated with primed seeds is their relatively short storage lifespan. This review aims to explore the biochemical, physiological, and molecular aspects of rice seed priming while proposing innovative techniques to extend seed longevity, improve stand establishment, and increase overall yield. Furthermore, understanding the molecular mechanisms underlying seed priming can lead to the development of more effective priming protocols. This could ultimately contribute to sustainable agricultural practices in regions vulnerable to climate variability.

Keywords

Seed Priming, Drought Tolerance, Biochemical Responses, Physiological Changes, Rice Seeds, Seed Longevity, Agricultural Practices, Stand Establishment

1. Introduction

Emergence and early seedling development are particularly susceptible to chilling stress in most rice cultivars [43]. Unlike other cereals, rice is a water-loving plant susceptible to drought stress [29]. The sustainability and productivity of transplanted-flooded rice are threatened by the depletion of water resources, labor shortage, and the water-intensive nature of rice farming [39]. Dry direct-seeded rice technology has been suggested as a way to optimize resource use efficiency, lower the need for water, save labor, and enhance environmental sustainability [22]. However, drought stress

hampers seed germination and delays seedling establishment in dry direct-seeded rice. Extreme drought stress can occasionally lead to a total suppression of seedling emergence [29]. When plants are stressed by drought, reactive oxygen species (ROS) are produced, which can harm plants by breaking down proteins, lipids, and DNA, potentially resulting in cell death [43]. Plants may withstand stress through the creation of metabolites and activation of the antioxidant system. Oxidative stress tolerance can be genetically controlled through conventional breeding and selection, transgene production, or

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Received: 6 August 2024; **Accepted:** 6 September 2024; **Published:** 18 October 2024



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physiological approaches such as seed priming, which is one of the most practical, efficient, and short-term methods for boosting seed vigor, timing germination, and the growth of seedlings of many crops under various abiotic stresses, including drought [22].

According to [43], experiments on priming types were conducted to ascertain the role of seed-priming on emergence, seedling growth, and associated metabolic events in a dry-direct seeded rice system. The study demonstrated that all seed priming treatments were effective in alleviating the damaging effects of drought stress, possibly due to improved starch metabolism and increased α -amylase activity in primed rice seedlings. According to [43], Seed priming is an effective strategy to enhance crop establishment in challenging conditions. However, the technique's adoption was hindered by the shorter shelf life of primed rice (*Oryza sativa* L.) seeds during storage. Storing primed seeds under high relative humidity conditions for longer than 15 days was found to be detrimental to rice germination and growth. In contrast, the longevity of non-primed rice seeds was not affected by storing them under various conditions for 15–60 days. It is nonetheless advised to store primed rice seeds under vacuum, low relative humidity, or low temperature settings to ensure excellent crop establishment. A study on dry rice seed also demonstrated that airtight bags, such as PICS bags and Grain-pro Super bags, could maintain rice seed quality better than jute bags and polypropylene bags. Sealed packaging containers exhibited significantly greater seedling dry weight, probably due to the reserved carbohydrate inside the rice seed as a result of reduced respiration and maintained moisture content until the 18-month storage period [37]. The respiration by the grain, insects, and fungi lead to a drop in oxygen level and an increase in carbon dioxide within the hermetic bag [17].

Seed priming is known to initiate typical metabolic developments in the early stages of germination, prior to radicle protrusion. The development of germination-promoting metabolites, osmotic adjustment, decreased imbibition time, enzyme activation, and metabolic reparation during imbibition are the main causes of higher, faster, and synchronized germination of primed seeds. In addition, plants that sprout from primed seeds show quicker cellular defense system activation, which promotes tolerance against subsequent exposure to environmental challenges in the field. However, limited information is available in the literature on the longevity of primed rice seed stored in hermetic bags. This study aims to fill the research gap and investigate the effect of hermetic storage on the longevity of primed rice seed.

Problem Statement

Seed priming is a method in which seeds are hydrated (control hydration or uncontrolled hydration) and dried to original moisture content but the actual emergence of radicle is prevented. Unequal plant stand and poor germination are major constraints in seeds under areas which receive erratic and low rainfall. This problem of poor germination can be overcome by sowing primed seeds. Seed priming improves

the germination ability of seed and ultimately improves plant stand in the field [17]. However, one of the major problems in priming technologies is the *limited storability of primed seeds*. The past research gap to fill after this study is *short storage period of primed seeds and the effect of hermetic storage on primed seed longevity is unknown*. Hence primed and re-dried rice seed storage longevity might be improved through hermetic packaging storage techniques and storage conditions.

Therefore, combinations of right quantity of priming methods and seed packaging techniques have to be developed to store primed seed. Such techniques will revolutionize farming in moisture stresses areas where farmers have low access to technologies [37]. However, conducting the priming operation, monitoring water uptake and careful drying are difficult to manage in large scale especially at farmers' level. Again, research has shown that primed seeds cannot be stored for more than few weeks due to reduced repair mechanisms present for DNA damage caused by progression in cell cycle during hydration [33]. When a primed seed is stored under conducive conditions (low temperature and low moisture) most of the beneficial effects of priming are retained. However, the storability of the primed seed per se is either improved or adversely affected, depending upon the initial physiological status of the seed [37].

Fogera National Rice Research and Training Center and Seed producing cooperatives that commonly produce rice seed of two upland ecosystem rice varieties *NERICA4*, *Fogera1* and a lowland ecosystem rice variety named '*Selam*'. Seeds of *NERICA4* and *Fogera1* rice varieties are always exposed to chilling or sensitive to cold stress so that it frequently aborts pollen during flowering time, which results in unfilled hulls which reduce the rice seed yield and quality. This is a great challenge to produce and disseminate the expected amount and quality of early generation rice seed country-wide in Ethiopia. Therefore, this review will highlight the storability of primed rice seed, to determine physiological seed quality, seedling establishment and yield of primed rice and to review the overview of the physiological, biochemical, and molecular alterations modulated by seed priming, enhancing seed germination and plant growth. Furthermore, the respective possible ways associated with seed priming-induced abiotic stress tolerance in plants will be assessed.

2. Drought Stress Effects on Rice Seed Quality, Seedling Establishment and Yield

Seed deterioration is the loss of quality (vigor and viability) due to aging and unfavorable environmental conditions, particularly higher temperatures, relative air humidity, and an increased oxygen/carbon dioxide ratio during pre-harvest (field weathering), harvest (handling), and post-harvest (storage) periods [17]. Drought (water deficits) stress is the

prime abiotic constraint, under the current and climate change scenario. Crop yield and food security would be drastically reduced by any additional rise of the stress. Due to a reduction in seed size and quantity, drought stress has a significant impact on seed yields. This ultimately affects the commercial trait "100 seed weight" and seed quality [35]. Drought stress disorders the normal physiological functioning, restricted growth and reduced productivity of rice plants [41]. Drought-induced malfunctioning of vital physiological processes includes diminished photosynthetic activity, decreased water use efficiency, low transpiration rate, poor stomatal conductance, reduced CO₂ concentration, imbalanced water relations and membrane impairment [35]. Rice is particularly vulnerable to the effects of chilling stress during the emergence and early phases of seedling growth. Under chilling stress, seed priming can be an effective strategy to improve rice germination and stand establishment [14]. Low temperature causes male sterility during reproductive development on rice production in Ethiopia, which generally lies at high elevations. Spikelet fertility was explained by both anther length and number of fertile pollen grains per anther under cold stress [11]. According to several studies [44, 32, 33]. Seed priming may be a crucial and straightforward method for enhancing seed germination, vigor, and stand establishment of crop plants under diverse abiotic stresses. Germination at the field level is irrelevant if rice is cultivated by transplanting since the technique raises rice seeds in ideal conditions, yet it is possible that seedlings cultivated from primed seeds will germinate and may grow vigorously. However, seedlings grown from primed seeds may grow vigorously, which could aid in production. In Basmati rice, seed priming with CaCl₂ increased the quantity of grains per unit area and the fertility of the tiller [27]. According to [27], there was a highly substantial positive correlation between grain yield and seedling emergence and growth at the nursery. When enough water is absorbed and the seed coat becomes soft and elastic, rice seeds will germinate [39]. Biotic and abiotic stresses caused by changes in climatic patterns bring about detrimental morphological, biochemical, physiological, and molecular changes that disturb the plant growth and development and ultimately the seed yield [33]. Drought stress is one of abiotic stresses that adversely affect seed-filling processes in all crop species, resulting in poor-quality seeds and reduced seed yields [36]. Similar investigations showed that chilling stress caused rice seedlings to accumulate more hydrogen peroxide and lipid peroxide while also causing irregular and delayed germination, poor seedling growth, decreased starch metabolism, and lower respiration rate [15]. Numerous seed priming techniques have been found to benefit rice under chilling stress in recent research. Through increasing α -amylase activity and soluble sugar content, seed priming improved the chilling tolerance of rice seeds during germination and growth [25]. According to this paradigm, preserving seed vigor and facilitating effective germination depend on the seed repair response [26]. Furthermore, malate synthase and isocitrate

lyase, which change fats into carbs, and antioxidant enzymes (POD, SOD, CAT, and GR), which scavenge reactive oxygen species (ROS), perform better when seeds are primed. According to some observations, priming lowers metabolite leakage, promotes early DNA replication and repair, enhances RNA and de novo protein synthesis [29], and helps repair chromosomal damage [37]. Seeds are subjected to harsh conditions during maturation, storage, and rehydration that cause DNA oxidation. This leads to nuclear DNA fragmentation and loss of integrity, which may be harmful to the genome and stop the cell cycle. Reactive oxygen species (ROS) are thought to be the main factor in single-strand breaks in DNA that affect seeds and prevent them from germinating. In plant cells, reactive oxygen species (ROS) are considered the primary cause of single-strand breaks in the DNA, having a detrimental effect on seeds and leading to germination failure (Bray and West, 2005). Therefore, DNA repair mechanisms, including homologous recombination (HR), base excision repair (NER and BER), non-homologous end joining (NHEJ), and reactive oxygen species scavenging, are now recognized as essential pre-germinative metabolic processes. Additionally, the degree of germination is correlated with the ability to repair DNA during seed rehydration [14].

2.1. Fundamental Processes Involved in Seed Priming

A pre-sowing procedure known as "seed priming" involves exposing seeds to a certain solution for a predetermined amount of time. This allows for partial hydration but prevents radicle emergence. The three stages of non-dormant seed germination are (I) imbibition, (II) lag phase, and (III) protrusion of the radicle through the testa, which happen when a dry seed is kept in water [2].

During seed priming, the seed's water supply is regulated. It raises the seed's moisture content below what is necessary for true germination. The seed cannot progress towards complete germination at this level, but it is sufficient to initiate many of the physiological processes linked to the early stage of germination (pre-germination metabolism) [24, 25]. However, after this point, drying back or re-drying to the original moisture content is required to preserve the positive effects of priming treatment without sacrificing quality due to quick seed deterioration [8, 33]. The seed can withstand desiccation before radicles develop, so priming can be followed by a dehydration phase to preserve the primed seeds. Returning to the original moisture level does not harm the seed. Phase I (imbibition) or II (activation) of the seed is drying, but phase III (growth) is too far along to permit a drying-back without causing damage to the seed. The vigor and viability of seeds are harmed by drying them after the radicles have begun to develop [8].

The storage and drying-back conditions affect how long primed seeds could be preserved by maintaining good characteristics. According to [9], a quick drying-back can change the soluble carbohydrates in seeds and shorten their ability to

withstand desiccation. Later longevity could be enhanced by a gradual drying-back [3]. Rehydration stimulates DNA repair and defense systems in seeds, reducing growth inhibition during seedling development. Seeds are subjected to a variety of unfavorable conditions during maturation and storage, which can lead to DNA oxidation, loss of DNA integrity, and disruption of the cell cycle [10]. DNA repair activities in embryos must be maintained at the right level in order to maximize the likelihood of successful germination and maintain the vigor of the seed. According to [43], antioxidants and DNA repair mechanisms, particularly NER and BER, are important pre-germinative metabolic activities.

Nonetheless, a number of post-priming procedures have been created to lessen the detrimental impact that traditional priming has on the lifetime of seeds [5]. The inherent variability of priming itself presents another difficulty since not all priming procedures will result in better seed germination performance and because improper priming conditions can cause protective proteins to degrade, making seeds more susceptible to stress [7]. Therefore, it is always crucial to identify the best priming technique that is specific to the plants in order to maximize germination performance and seed stress tolerance. Using the "hydro-time concept," which can also be helpful in avoiding the drawback of reduced lifetime due to extended treatment, the priming regimens can be improved. This is so because the relationship between seed water potential and the amount of time needed for radicle emergence is explained by the "hydro-time concept." When assessing a seed lot's physiological status, hydro-time analysis is helpful since all of the factors included in the analysis might highlight any potential anomalous responses in terms of germination and seedling establishment in stressful environments [4]. Digital image technology (DIT), a non-invasive technique, also has great potential for accurate and automated assessment of seed morphological and physiological features, and can be widely utilized for accurate analysis of vigor as well as seed purity [6].

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Biotic and abiotic stresses caused by changes in climatic patterns bring about detrimental morphological, biochemical, physiological, and molecular changes that disturb the plant growth and development and ultimately the seed yield [13]. Drought stress is one of abiotic stresses that adversely affect seed-filling processes in all crop species, resulting in poor-quality seeds and reduced seed yields [36]. Similar investigations showed that chilling stress caused rice seedlings to accumulate more hydrogen peroxide and lipid peroxide while also causing irregular and delayed germination, poor seedling growth, decreased starch metabolism, and lower respiration rate [15]. Numerous seed priming techniques have been found to benefit rice under chilling stress in recent research.

3. Physiological and Biochemical Aspects of Seed Priming

3.1. Physiological and Biochemical Changes

Many physiological and biochemical changes are responsible for the enhanced vigor and germination of primed seeds. These include damage repair, improved mobilization of reserves into growing seedlings, a shorter imbibition time required for the onset of RNA and protein synthesis, polyribosome formation, increased total RNA and total protein content, improved membrane integrity, control of lipid peroxidation, increased sugar content, protein and nucleic acid synthesis, removal of inhibitors like abscisic acid, efficient production and utilization of germination metabolites, and increased activity of enzymes such as alpha amylase, acid phosphatase, esterases, dehydrogenases, isocitrate lyase, protease, peroxidase, catalase, glutathione reductase, superoxide dismutase and ROS production [23]. The reactive oxygen species (ROS) functions as signalling molecules in plants thus regulating growth and development, programmed cell death and hor-

more signalling. Reactive oxygen species (ROS) such as superoxide radicals (O_2^-), Seed Vigour and Invigoration 83 hydrogen peroxide (H_2O_2) and hydroxyl radicals (OH) are generated as a result of redox reactions in seeds. Seed priming treatment strengthens the ROS mechanism in the seeds facilitating better performance of primed seeds [1].

Physiological, Biochemical, and Molecular Responses to Seed Priming

Water stress causes a variety of physiological, biochemical, and molecular reactions in plants. Research indicates that in addition to their common hormonal responses, plants also display biochemical and molecular reactions when faced with various stresses as part of their stress tolerance mechanisms [31]. Seed priming influences physiological and biochemical processes (DNA repair, synthesis of proteins and nucleic acids, antioxidant activity, and energy metabolism), which increases the capacity of seedlings to withstand stress [15]. It has been shown that seed priming increases plant species' resistance to abiotic stresses such as drought, salt, cold, and heavy metals [14]. The period between seed planting and seedling emergence plays a crucial role in stand establishment of crops. Seed priming has been used to improve germination rate and uniformity [17]. Primed seeds usually have more and uniform germination due to decreased lag time of imbibitions, activation of enzyme, enhanced germination metabolism, improved repair processes, and osmotic adjustment [14].

From priming processes, Phase I is characterized by the priming memory activation. During this phase, DNA and mitochondria are repaired, proteins are synthesized, stress response genes are stimulated, and signaling pathways are regulated. Phase II is the most critical phase, whereas the major metabolic and cellular activities are increased, resulting in germination initiation. In this phase, a series of proteins such as those related to ROS scavenging and signaling, storage, and stress response are synthesized in the embryo using existing and new messenger ribonucleic acid (mRNA), and the mitochondria and DNA are also synthesized and repaired. In Phase III, water and oxygen absorption increases, major reserve material mobilization occurs, embryonic axis elongates, and finally radicle protrudes from the coat of seed to complete germination and to start the post-germination stage [30, 35]. The benefits of seed priming include the upregulation of proteins and genes involved in cell division, cell wall modification, transcription, reserve mobilization, translation, oxidative stress response, and water transport, wherein DNA and membrane repair are better than normal imbibition [21].

When the primed seeds are sown, the imbibition phase and lag phase of water absorption are shortened [20]. Seed priming reduces the physical resistance of the endosperm during imbibition, repairs membranes, develops immature embryos and leaches emergence inhibitors [30, 2]. Therefore, the seedlings emerge faster, grow more vigorously, and do better in adverse conditions [35].

3.2. Effects of Seed Priming on Storage Longevity, Seedling Growth and Yield of Rice

Physiology of primed seeds is different from non-primed seeds. Viability of seeds is lost due to decrease in respiration rate, increase in RQ and malfunction of electron transport chain. Once the germination process is stopped, respiration starts to decline, and several other abnormalities such as activation of DNase, production of free radicals and degradation of protein occur. These lead to loss of seed viability [43]. It was observed that in many cases, primed seeds lost their viability during storage [16]. Commercial success with primed seeds depends on storability of it. If the viability of seeds lost within shortest time, then commercial success is not achievable with priming. Viability of rice seeds declined within 15 days of priming at storage temperature of 25 °C [16]. Primed rice seeds stored under vacuum condition either low or room temperature and at room temperature with low humidity did not lose their viability. It showed that interaction between cultivars and technique of seed priming has great impact in influencing the storability of primed seeds [43]. So, seed viability could be extended even in primed seeds through choice of suitable rice cultivars and use of suitable seed priming technique.

Sowing primed rice seeds was found to be advantageous in shortening the numbers of emergence, heading, and maturity days. Reduction in the maturity period of rice by 14.1 days is a significant phenological achievement. This achievement could immensely benefit farmers through pre-empting the detrimental effects of terminal moisture stress, which has become a serious rice production bottleneck at Fogera plain due to climate change that caused the occurrence of erratic and scarce rainfall especially at the last phase of the growth period of the plant. This study was in agreement with [19], who reported that reduced germination and poor seedling stand is the first and foremost response of plants to water shortage. Seed priming efficiently improved emergence and seedling growth performance of dry direct-seeded rice under water deficit conditions. A readily available food source for seedlings during germination may contribute to primed seeds' superior capacity to finish the germination process quickly and adapt to water-limited settings [43]. On the other side, the ability of plants to degrade starch into soluble sugars under water limited conditions probably plays a key role in their ability to survive and grow faster under stress. When rice germinates, amylase activity is strongly stimulated [15], however, this activity begins to appear even earlier, during seed maturation. Drought stress considerably decreased the total soluble sugars in rice cultivars and α -amylase activity [43]. The appropriate research output determined with the study encompasses using pre-germinated and primed rice seeds respectively where the highest grain yields were recorded when pre-germinated rice seeds were planted at farmers' sowing time followed by planting seeds soaked for 24 hours

and dried for 24 hours at farmers' planting time [40].

4. Conclusion and Recommendation

Seed deterioration is obvious process in seed development, therefore; it is necessary to retard the process through mechanisms that trigger physiological, biochemical and molecular processes. Seed priming one of these techniques that does not require expensive technology of which hydro-priming is the most cost- effective approach. In addition to priming, for drought stress seems to be the use of appropriate factors at various stages of plant development. Methods developing in the direction of imparting higher drought tolerance on plants include: supplying plants with silicon, exogenous application of growth regulators or osmo-protectants and seed priming which are particularly promising in countries where cultivation of GMOs is highly restricted.

Seed priming contributes many beneficial effects for the seed and seedling establishment as well when seeds are sown immediately after priming. However, when there exist environmental stress like drought, it is not advisable to sow primed seeds rapidly because primed seeds will lack adequate moisture in the soil and fail to germinate subsequently loss in yield like particular example in Ethiopian case rice crop which needs adequate water for seed germination. Therefore, re-drying primed seeds to the original moisture content and packaging in hermetic containers is recommended. However, how imbibition of water create suitable condition for rice seed on DNA level, and how important characters of rice seed are retained needs future study. Hence, the effects of drought need to be investigated in future research involving various physiological, biochemical and molecular approaches.

Abbreviations

DNA Deoxyribonucleic Acid

Author Contributions

Yilikal Melak Assaye is the sole author. The author read and approved the final manuscript.

Conflicts of Interest

The author declares no conflicts of interest.

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