Crop improvement: a seed priming approach

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Abstract

Seed priming is used to achieve different objectives of crop production. These include better germination, improved growth and yield as well as better tolerance to different environmental stresses. Some of the methods employed work for some crops while they are detrimental to others. The present work x-rayed different aspects of priming technology starting from its types and ends with its direct and indirect effects. It started with explanation of different types of priming media: hydro-priming, osmo-priming, hormonal and chemical priming. It then examined optimum priming concentration and duration. It also looked into how seed priming improves yield and yield quality of different crops. It further examined how seed priming aids direct seeding, confers tolerance against drought, salinity and low temperature stresses in plants. In addition, it discussed how thermo-inhibition and oxidative stress are alleviated with seed priming. In the same vein, it explained some of the mechanisms of priming operation and answered the question on whether seed priming is a source of stress to seeds or not. Moreover, it justifiably elucidated biochemical and enzymatic changes, pattern of genetic expression, and proteomics of primed seeds and their resulting plants. Finally, it answered the question on whether seed priming has direct or indirect effects on plants. The information contained in this paper will aid understanding of seed priming technology and make transition from its theoretical knowledge to practical use an easy task.

Key-words: Seed Priming, Crop Improvement, Environmental Stresses, Oxidative Stress, Yield Improvement

Introduction

Seed priming involves controlled soaking of seeds in water or solutions of low water potential until germination sensu stricto stage is reached while radicle emergence is prevented. The seeds are then thoroughly washed with water to remove all the traces of the priming chemicals from them. The seeds are then dried back to their original moisture level so that they can be stored till the time of sowing like untreated dry seeds (McDonald, 1998). Seed priming can be achieved
through exogenous use of phyto-hormones like GA3 (Ghobadi et al., 2012). In the same vein, seeds can be primed in distilled or ordinary water (hydro-priming) as well as solutions of different osmotic salts (osmo-priming). This technology is used for overcoming problems of low yield, poor germination and erratic seedling establishment (Ahmadi et al., 2007). During priming process, we must consider the optimum concentration for success of the priming to avert germination retardation or death of seeds through chemical toxicity (Basra et al., 2007). Furthermore, priming duration should not exceed the optimum period (safe limit) to have optimum result from any priming treatment used. The safe limit is crop and species dependent and should be guarded to prevent getting negative results because effectiveness of seed priming hinges on treatment duration (Ghassemi−Golezani et al., 2008). Seed priming is effective in yield improvement as well as quality enhancement (Rehman et al., 2011). Also, seed priming improves the performance of rice plants under direct seeding system which can be wet, dry or water seeding. This farming system has been in operation for rice production in developing countries since 1950 (Pandey and Velasco, 2004). Moreover, seed priming is now being used for alleviation of moisture stresses which is a limiting factor in crop production. It has been established that breeding programmes have not yet produced the expected result in improvement of stress tolerance in crops especially new varieties (Lafitte et al., 2004). Therefore, seed priming is now used as a potential strategy against drought stress in arable crops like rice though its effectiveness is limited by drought severity, crop type and cultivar (Yuan−Yuan et al., 2010). Similar to drought stress, general use of seed priming treatment can reduce salinity stress(which is a great problem combating crop production in different continents) to the barest minimum (Afkari, 2010). For instance, salicylic acid priming alleviated salinity stress in triticale (Zadehbagheri, 2014). Moreover, seed priming can be used to remove thermo-inhibition in seed germination (Schwember and Bradford, 2010) and improve seed performance under low environmental temperature (Lin and Sung, 2001). For instance, chitosan priming has been used for improvement of morphological characteristics of maize seedlings under low temperature stress (Guan et al., 2009). The stress tolerance conferred on plants resulting from seed priming is through responsive and effective anti-oxidative system (Guan et al., 2009). Furthermore, priming technology conferred tolerance to stress on plants because priming process is a pre-germination exposure to stress which leaves stress memory in the seeds to tolerate future stresses in their environments (Bruce et al., 2007). Finally, the effect of seed priming treatment is direct on the treated seeds while growth and yield improvements are the indirect results of the technology. This is because better growth and yield are achieved from seed priming through having higher number of seedlings, better seedling establishment and vigour (Ghassemi–Golezani et al., 2010).

EFFECTS OF GROWTH REGULATOR PRIMING ON CROP PRODUCTION

The use of different chemical agents for priming seeds of different plants to improve their growth and economic yield has become popular in different parts of the world. Seeds could be primed with plant growth regulators or phyto-hormones and the priming process is called hormonal priming. Phyto-hormones are exogenously used in priming process because the endogenous ones have been found to be effective in growth and development activities of plants. For instance, 50ppm GA3 improved root and shoot length as well as the final yield when it was used for priming wheat seeds (Cross-Alborz and Sardari cultivars) for duration of 24hours under normal irrigation condition (Ghoohoestani et al., 2012). Similarly, salicylic acid (SA) priming at lower concentrations has been effectively used in enhancing hydrolase activities and that led to increase in breakdown of food reserve and consequential early germination of the seeds (Shakirova et al., 2003). In the same vein, salicylic acid and ascorbic acid priming were used to reduce electrolyte leakage (Khan et al., 2011). Priming with low SA(50ppm) concentration has also been found to improve germination parameters of melon (Cucumis melo L.) by improving biochemical activities of the seeds during priming process (Basra et al., 2007).
Finally, 100ppm kinetin priming has been found effective for better yield improvement of MR219 rice variety and can be a better replacement of pre-germination treatment because of better yield (Kareem et al., 2020a).

An indirect way of getting natural plant growth chemicals is through the use of plant growth promoting rhizobacterial (PGPR). These chemicals are effective as priming agents as stated earlier. For instance, the use of Azotobacter, Azospirilulum and the combination of the two were used to pre-germinate maize seeds and the treatment resulted in high maize yield and dry matter accumulation although the peak performance was from Azotobacter treatments (Sharifi and Khavazi, 2011). In a similar case, PGPR increased yield and dry matter accumulation of rice (Sudha et al., 1999), barley (Fiahin et al., 2004), wheat (Cakmaki et al., 2007), Canola (De Freitas et al., 1997), sugar beet (Cakmaki et al., 1997) and sugar cane (Sudha et al., 1999). These established results demand understanding of PGPR operation mechanism. On its mechanism, it has been suggested that it was through production of phyto-hormones which enhance stress tolerance, nitrogen fixation and stimulation of nutrient uptake (Sindhu et al., 1999). Another view was that it operates by increasing the supply of primary nutrients to the host plants (Wu et al., 2005) and synthesizes antibiotics, enzymes and fungicidal compounds (Ahmad et al., 2008).

**EFFECTS OF HYDRO-PRIMING AND OSMO-PRIMING ON CROP PRODUCTION**

Distilled water, ordinary water as well as different osmotic salt solutions can be used in pre-sowing treatment of seeds of different varieties and species. Priming with water is called hydro-priming while priming with osmotic salts is referred to as osmo-priming or osmotic-priming. Common osmo-priming salts are polyethylene glycol (PEG) 6000 or 8000, potassium chloride, sodium chloride, magnesium chloride and so on. Use of hydro-priming or osmo-priming proffers solutions to problems of low yield, poor seed germination and non-uniform seedling establishment in different crops. However, hydro-priming is easier and cheaper than osmo-priming and it is helpful in improving both germination and yield of different plants. It also competes favourably with osmo-priming and performs better in many occasions. For instance, hydro-priming has been effectively used in improving germination and seedling emergence of lentil (Ghobadi et al., 2012). Furthermore, when hydro-priming and some osmotic salt solutions were used in pre-sowing treatment of forage sorghum, hydro-priming competed perfectly with the rest priming agents and produced the highest leaves (Shehzad et al., 2012). Similarly, when hybrid sunflower (Hysun-33) was primed with aerated water (hydro-priming), saturated gummy bags (matri-priming) and 0.1% sodium chloride (osmo-priming), it was found that yield contributing factors and achene yield were highly enhanced by both osmo-priming and hydro-priming while plant height and achene oil contents were not improved (Hussain et al., 2006).

The use of seed priming for germination improvement, seedling establishment and yield increase is not limited to cereals or forage crops alone. Rather, the technology has been found useful in legumes like soybean when PEG 8000 was used for its priming treatment (Arif et al., 2008). For wheat, PEG, KCl, potassium hydrogen phosphate or distilled water can be used to increase its dry matter production, yield and yield components (Yari et al., 2011). Furthermore, osmo-priming has been effectively used to increase the final emergence percentage, root and shoot dry weight, root and shoot length as well as root to shoot ratio of wheat (Basra et al., 2007). In the same vein, growth and yield status of fine rice has been improved with 30ppm salicylic acid priming (Farooq et al., 2007). Enhancement of root and shoot as well as the final yield by hydro- and osmo-priming are the results of increased mitotic cell division and cell enlargement occasioned by expansion of assimilate sinks (Farooq et al., 2007).

**EFFECTS OF PRIMING MEDIA CONCENTRATION ON PRIMING EFFECTIVENESS**

The concentration of a priming solution, in many occasions, determines the success of priming technology. This varies with different crops (Table 1).
### Table 1. Optimum concentration of priming solutions for some plants.

| CROP               | CHEMICAL | CONCENTRATION | CONDITION | REFERENCE                           |
|--------------------|----------|---------------|-----------|-------------------------------------|
| Indica hybrid rice | PEG      | 20% (w/v)     | Drought   | (Yuan−Yuan et al., 2010)            |
| Wheat              | Kinetin  | 100ppm        | Salinity  | (Iqbal and Ashraf, 2006)            |
| Myricaesculenta    | GA₃      | 100ppm        | Normal    | (Bhatt et al., 2000)                |
| Rice               | Salicylate | 30ppm      | Normal    | (Farooq et al., 2005)               |

If the concentration is below the minimum threshold, priming treatment fails to initiate the expected physiological and biochemical processes of germination. On the other hand, if the concentration of the priming solution is too high or the duration of process is too long, seed germination will either be retarded or hampered completely as a result of toxicity (Basra et al., 2005).

The fact that different priming solutions have the same concentrations does not guarantee their similar performance when they are used for seed treatment. This applies to all the chemicals employed whether hormones or osmotic salts. For instance, wheat seed priming with 20ppm salicylic and ascorbic acid for 24h was found to increase phosphorus, potassium and soluble sugar contents (Khan et al., 2011). Contrary to 20ppm of salicylic and ascorbic acid used for wheat, priming with 5ppm IAA and GA₃ were found to be optimum and very effective for seed germination and seedling growth in cowpea (Audi and Mukhtar, 2009). The issue of optimum concentration is not only restricted to hormonal priming alone but it is also applicable to osmotic priming. Low concentration problem may be corrected through extension of priming duration while toxicity is yet to get any remedy.

### EFFECTS OF PRIMING DURATION ON EFFECTIVENESS OF PRIMING PROCESS

Controlled imbibition of water which forms the basis of seed priming technology is inherently affected by soaking duration. Priming duration along with optimum concentration of any priming media used is a very important factor that determines germination success and seedling establishment. This is because water imbibition of the seeds during priming process is directly related to priming duration. It is an established fact that effectiveness of seed priming on seed invigouration and final yield are dependent on the treatment duration (Ghassemi−Golezani et al., 2008). The period of priming may be beneficial or detrimental to the seeds or resulting plants from the treatment. For instance, increased germination, better seedling establishment and higher yield were realized through 7 to 14 hour priming of pinto seeds while longer duration was detrimental to pre- and post- germination lives of the plant (Ghassemi−Golezani et al., 2010). Furthermore, priming for shorter duration has been found to result in low leachate leakage and electrical conductivity as a result of seed protection and minimization of cell wall damage. It has been explained that primed seeds imbibe water until a plateau is reached and then there would be a little change to circumvent the protrusion of radicle (Farahani and Maroufi, 2011). This has been confirmed by Ghassesemi- Golezani et al. (2010) and they added that the process will lead to positive response of the primed seeds while priming beyond the described level would be disastrous to the seeds and the resulting plants.

On priming against environmental stress, Farahani and Maroufi (2011) submitted that a 12-hour hydro-priming was highly effective for production of Basil (Ocimumbasilicum L.) under salinity stress. The researchers further asserted that the longer the priming duration; the better the ability of the resulting plants in withstand salinity stress as long as the priming duration did not exceed 12 hours. Nevertheless, variations do occur on the basis of seed types and the presence of growth inhibitors. This is because thickness of the
seed coat varies from one plant to another. The problem of seed coat thickness is mainly evident in tree crops where the seeds have to be treated first for removal of dormancy. In priming codia seeds (*Cordia millenii*) which is a species of timber tree, a three or four day osmo-priming was found most effective in breaking the seed coat to give the highest emergence percentage while hydro-priming for two days gave better results than osmo-priming for the same duration (Adebisi et al., 2011). In the same vein, when seeds of bread wheat were primed with PEG for a period of 12hours, emergence percentage as well as economic and biological yield parameters were enhanced (Yari et al., 2011). It has also been found that priming rice seeds with 100mM calcium chloride or 40% PEG 6000 should not exceed 48hours while priming with 100ppm kinetin should not exceed 24 hours to achieve effectiveness in the priming treatment under normal and drought stress conditions and avoid wastage of resources (Kareem et al., 2020b). Similarly, in wheat cultivars (Cross-Alborz and Sardari), Ghabadi et al. (2012) discovered that a 12-hour priming with PEG$_{6000}$ (-0.3MPa) resulted in higher germination percentage, appreciable root and shoot lengths as well as higher weight of roots and shoots. The result of higher germination was explained by Jie et al. (2002) through priming rye seeds with PEG$_{6000}$. They established that the production of super oxide dismutase (SOD) and peroxidase (POD) were chiefly responsible for higher germination recorded.

**EFFECTS OF SEED PRIMING ON YIELD IMPROVEMENT AND YIELD QUALITY**

The utmost target of plant production is the economic yield in form of grains or fruits except when folder production is the objective of the cultivation. All agronomic, genetic as well as physiological manipulations focus their achievements on yield and quality improvement. In the history of research on priming, one of the successful means used in such researches was hydro-priming (the use of water as priming agent for seeds). For example, hydro-priming of pinto bean (*Phaseolus vulgaris* L.) has been documented to have resulted in appreciable increase in yield and yield components. The result was attributed to improvement in the seedling vigour achieved through the priming treatment (Ghassemi–Golezani et al., 2010). In the same vein, the use of zinc sulphate priming (osmo-priming) was used to enhance yield in maize production (Afzal et al., 2013). Similarly, general use of osmo-priming and hormonal priming led to improved rice yield (Kareem et al., 2019). Also, specific use of calcium chloride priming improved both yield and yield attributes of rice (Rehman et al., 2011). Similar to rice performance, a 12h priming of wheat seeds has been found to have increased the crop yield and its harvest index (Hussian et al., 2013). Though all the cited cases involved crop production under normal conditions, crops under environmental stresses also showed improvement in yield like the case of rice (Tilahun–Tadesse et al., 2013).

Despite the fact that yield increase could be gained through seed priming, there is still need for the produced grains to be of higher quality too. Otherwise, the technology would have been regarded as being defective. But this aspect of yield quality is equally catered for by priming technology. For example, rice grains resulting from osmo-priming or hardening have been found to have higher levels of calcium (Rehman et al., 2011), potassium and phosphorus. These results were attributed to early root development and luxuriant growth of the resulting plants which aided better absorption of the nutrient elements that were needed for filling grains and their development (Ajouri et al., 2004).

**ROLES OF SEED PRIMING IN DRY DIRECT SEEDING**

Dry direct seeding is a form of planting which involves planting of seeds on the field directly without passing through nursery stage. Direct seeding could be wet seeding, dry seeding or water seeding. Wet seeding is achieved through sowing pre-germinated seeds on puddled soils. As for dry seeding, it occurs by sowing dry seeds on dry fields that have minimum water requirement for seed germination. Finally, water seeding is a method of direct seeding that requires planting dry or pre-germinated seeds in standing water. The system has
been in use for rice production in developing countries since 1950 (Pandey and Velasco, 2004). Nevertheless, Southeast Asia only resorts to dry seeding method during dry season when water availability becomes a problem. Despite the fact that dry seeding or generally direct seeding in rice production produces only 23% of the rice produced globally, Australia, the United States and Europe have now adopted the use either wet or dry seeding for rice production (Pratley et al., 2004). The practice of dry seeding is the practice in rain fed upland and low land areas of Asia as well as flood prone areas while wet seeding is the common practice in the irrigated areas of the same continent (Azmi et al., 2005).

Dry seeding or direct seeding of any form has several edges over the traditional transplanting method (Singh et al., 2005). Among these advantages is that dry or direct seeding has a significant reduction in production cost because the labour cost for puddling the fields as well as final transplanting of the seedlings to the final destination is circumvented (Farooq et al., 2005). Moreover, both direct seeding and transplanting produce similar yield despite the problems associated with transplanting. In addition to the mentioned advantages of dry seeding, planting of seeds is easier and faster with less water consumption than that of pre-germination (Bhushan et al., 2007). It is also more conducive to mechanization (Farooq et al., 2006) and the plants flower earlier (Farooq et al., 2006) with less methane emission (Balasubramanian and Hill 2002).

One of the major problems that can impede the achievement of higher yield in dry seeding method is crop establishment which is one of the yield components in rice production. The final plant population determines, to a large extent, the amount of grain yield that will be produced per unit area. However, success in crop establishment hinges on seeds of high quality which can emerge on time under different field conditions (McDonald, 1998). When crops emerge early, plant stands with higher vigour result. This then provides better root for anchorage which subsequently improves absorptive capacity of the roots (Watanabe, 1997). The observed problem of seedling establishment could be physiologically solved with the use of pre-sowing seed treatment (seed priming). This comes through seed soaking in aerated water or solution of low osmotic potential to give partial hydration of the seeds so that germination processes will begin without radicle emergence (Farooq et al., 2009). Direct effect of seed priming is directly felt on the seedlings at the early stage of their growth and development and that effect is converted to increase in number of tillers, productive tillers, panicles, filled grains and better seed weight. All these advantages finally result in higher yield of rice (Mohanasarida and Mathew, 2005b).

**ALLEVIATION OF DROUGHT STRESS THROUGH SEED PRIMING**

The most important environmental factor for living organisms is moisture availability. It determines the habitat of different plants and animals as well as their survival. When water becomes a limiting factor of crop production, solving the problem becomes a sine qua none to have success in production of any crop of interest. For instance, the nature of rice plant with the exception of upland varieties is to grow as a semi-aquatic plant because of its high water demand. Therefore, it is very sensitive to water deficit during its production. Problems that ensue from this situation are majorly physiological and, therefore, manifest morphologically in the plants. These problems have consequential effects on the final yield of the crop in question. The problem of water deficit is perennial in some places while it is ephemeral in others. Despite the sensitivity of rice to moisture stress especially at the reproductive stage of its life, it can tolerate acidity and salinity moderately. Attempts to curb the problem of moisture stress have been made through breeding but the level of tolerance needed is yet to be achieved in the present improved germplasm. Since the target of tolerance is yet to be met through breeding, there is dire need for a better and simpler intervention which can induce tolerance in the plants without any repercussion. At the present,
the simplest and most effective technology for this is seed priming which has been established to be meeting the objective for which it was devised.

Seed priming is a potential technology against drought in rice but depends on cultivars and limited by severity of the drought (Yuan–Yuan et al., 2010). This is because severe drought can inhibit germination and kill emerging seedlings. Among the viable chemicals that can induce moisture stress tolerance in cereals is potassium hydrogen phosphate (KH$_2$PO$_4$). This has been proven to aid better germination and seedling establishment along with other germination attributes (Yagmur and Kaydan, 2008). This outcome of priming has been attributed to better mobilization of seed reserves through efficient water uptake by the germinating seeds (Soltani et al., 2006). Moreover, alleviation of drought stress effect on physiology of rice has been achieved through abscisic acid (ABA) priming (Majeed et al., 2011). The mechanism of operation here involves decrease in GA$_3$ concentration in the plant. This then maintains water budget, improves osmoregulation by increasing proline accumulation, increases stomatal resistance and aids early maturity through increase in the rate of grain filling (Majeed et al., 2011). Moreover, improvement of drought tolerance in rice has been achieved by priming rice seeds in 14% (w/v) potassium chloride solution (Du and Tuong, 2002). In the same vein, osmo-priming has been used for priming rice seeds in drought prone areas and it resulted in faster emergence with high uniformity which finally led to realization of higher yield (Harris and Jones, 1997). Furthermore, 48 hour priming of rice seeds(MR219) with 100mM calcium chloride or 40% PEG6000 or 24hour priming with 100ppm kinetin is effective under drought stress condition (Kareem et al., 2020b). It could be summarily said that better seedling establishment that can confer better drought tolerance on rice plants could be achieved through seed priming technology. A proof of this is that when potassium hydrogen phosphate (KH$_2$PO$_4$) was used for priming cereals like triticale, it induced drought tolerance on the treated cultivar (Yagmur and Kaydan, 2008) through better mobilization of seed reserve as a result of efficient water uptake by the germinating seeds (Soltani et al., 2006).

ALLEVATION OF SALINITY STRESS THROUGH SEED PRIMING

In eco-physiology of plants, salt stress is one of the major hindrances against the expected performance of different crops though they may be genetically high yielding types. Moreover, salinity stress is now an important environmental factor obstructing seed germination and seedling establishment (Almansouri et al., 2001). Attempts to solve this problem have led plant physiologists to explore different avenues of which seed priming is one of the most potent technologies. The potential of seed priming has been proven by Finch–Savage and Leubner–Metzger (2006) who stated that when seeds were hydrated and then dried before radicle protrusion (seed priming), the seeds would store biochemical information that could alleviate germinating seed problems as well as the problems of the succeeding plants under stress conditions. An instance of his discovery was found when potassium nitrate was used as the priming agent for two soybean cultivars in glass house and field experiments. Seed priming subdued the effect of stress and consequently there were improvements in germination percentage, seedling emergence, radicle and plumule length, plant height, leaf area, seedling dry mass and total biomass production of the resulting plants (Ahmadvand et al., 2012). In the same vein, the use of potassium nitrate for priming sunflower seeds (Helianthus annus) resulted in improvement in all its germination parameters (Tzortzakis, 2009) and malondialdehyde concentration (Farhoudi, 2012). Moreover, different priming treatments have been used to reduce salinity stress to the barest minimum (Afkari, 2010). For instance, salicylic acid priming has been used to alleviate salinity stress in triticale (Zadehbagheri, 2004). However, the use of methyl jasmonate, chloroethyl phosphoric acid and ethylene releaser as priming agents to reduce induced oxidative stress in maize has not been effective with the exception of ethylene which improved biomass production of maize seedlings (Carvalho et al., 2011). This is an indication that ethylene is fundamental in conferring stress tolerance to maize which can be explained by other biochemical mechanisms but not through changes in antioxidant system (Carvalho et al., 2011).
Nevertheless, the use of salicylic acid for priming Faba beans has been used to improve salinity tolerance of the crop (Azooz, 2009). This has been attributed to enhancement of catalase (CAT), ascorbate peroxidase (APX), peroxidase (POD) and glutathione reductase activities. In the same vein, priming with 0.25mM and 0.5mM salicylic acid was effective in improving germination and salinity tolerance of Fenel (Foeniculum vulgare) (Farahbakhsh, 2012). Therefore, Horvath et al. (2007) considered salicylic acid as a potential growth hormone for alleviating abiotic stress for which salinity stress is a part.

Although salinity stress causes reduction in water potential of the treated seeds which eventually reduces imbibition rate of sown seeds as well as their germination, salicylic acid priming could be used to improve germination as well as dry matter accumulation (Ghoohestani et al., 2012). Similarly, priming with 15µM and 20µM salicylic acid were found effective in conferring salt tolerance on Fenugreek plant (Pour et al., 2012). Tolerance against salinity stress which salicylic acid priming conferred on plants was attributed to increase in cell division in the apical meristem of the root which gave opportunity for better absorption of nutrient and water with consequent better growth. Moreover, priming with PEG6000 (Polyethyl glycol) has been effectively used to improve seed germination and seedling establishment to confer tolerance on the resulting plants in an extreme saline environment (Fuller et al., 2012). The effectiveness of seed priming here has been attributed to synthesis of nucleic acids, proteins, enzymes as well as increase in respiratory activities and utilization of energy reserves (Cantliffe, 2003).

In a similar case, germination problem of alfalfa in saline environment, arid and semi-arid areas was solved through a 12-hour manitol priming (Amooaghaie, 2011). The problem might have been alleviated through enhancement of catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) activities as well as increase in proline (cytosolute) production accompanied by reduction in malondialdehyde level and decrease in electrolyte leakage (Amooaghaie, 2011).

Finally, osmotic and hormonal priming could be used to improve the potential of salt tolerant genotypes of some crops like Faba beans (Azooz, 2009). This implies that desired traits that are inherent in some cultivars could be further improved through exploration of seed priming technology.

**IMPROVEMENT OF THERMO-INHIBITION AND LOW TEMPERATURE STRESS TOLERANCE THROUGH SEED PRIMING**

Seed priming is one of the potential techniques used in solving germination problem which results from thermo-inhibition (germination failure at temperature below the upper limits for seedling growth) or any other cause. Thermo-inhibition can cause delay or absolute prevention of germination with consequential reduction in seedling emergence and establishment. It also results in diminished yield and multiple harvests that can reduce the quality of the crop with consequential profitability reduction. However, this problem was solved in lettuce through seed priming (Schwember and Bradford, 2010). Therefore, the problem could be effectively solved in other crops too.

Differences in climatic conditions of different parts of the world are important determinants of what to plant, how to plant and when to plant in order to achieve food security in any part of the globe. The eco-physiologists have a very great concern for solving this complex environmental problem. This is because some parts of the world are created to be very cold (very low temperature) while others are of opposite nature and both of them constitute serious abiotic environmental stresses for plants. Seeds have specific optimum temperature at which they can germinate based on crop types and cultivars. Without meeting the requirement of optimum temperature, the expected result will become elusive. Solving this low temperature problem has led plant physiologists to exploring seed priming technology. This is still in the realm of what was stated before that seed priming could improve seed germination performance under low environmental temperature (Lin and Sung, 2001). For instance, chitosan priming was used to lessen the detrimental effects of low temperature stress on root and shoot lengths,
dry mass, germination index and mean germination
time in maize (Guan et al., 2009). It was also found
that malondialdehide (MDA) level was decreased,
relative permeability of the plasma membrane was
low, concentrations of soluble sugar and proline
were increased and activities of peroxidase and
catalase were increased.

Better tolerance to low temperature stress
could be achieved by priming seeds with
combination of osmotic chemicals and phyto-
hormones as against using a single priming agent.
This was proven to be very effective when
potassium nitrate was supplemented with methyl
jasmonate or spermine in a single priming process
of musk melon (Korkmaz et al., 2005) and water
melon (Korkmaz et al., 2004) and the treatment
resulted in high germination percentage. The
reason behind the success of jasmonate or its esters
could be because jasmonates induce gene encoding
proteinase inhibitors that are involved in
lipooxygenase and flavonoid biosynthesis which are
responsible for plant defence mechanism against
stressful conditions (Creelman Mullet, 1997).

Nevertheless, the use of a single type of chemical
could still be judiciously used to stimulate the
plants against cold stress. For instance, when six
varieties of *Phaseolus fulgaris* seeds were primed
with 10^{-4}M of salicylic acid for a period of six
hours, it resulted in stimulation of all the aspects of
growth right from germination to seedling stage
despite the fact that the production was under cold
stress. The performance of salicylic acid was
attributed to modification of enzymatic activities
that were responsible for either biosynthesis or
break down of biochemical substances which may
be promoters or inhibitors of growth (Gharib and
Hegazi, 2010).

THE USE OF SEED PRIMING FOR
REDUCTION OF OXIDATIVE STRESS IN
CROPS

Oxidative stress is the problem posed by free
radicals and the reactive oxygen species (ROS). It
is caused by imbalance between the pro-oxidants
and the anti-oxidants arising from adverse
environmental conditions and leads to potential
damage because of increase in the level of
intracellular ROS levels (Sharma et al., 2010). The
level of oxidative stress is normally measured
using lipid peroxidation.

Lipid is so important in the bodies of animals
and plants that it will be so difficult for either of the
two kingdoms of living things to be independent of
it. Apart from being an efficient energy source, it is
equally a part of cell membrane and nerve tissue
and it provides thermal and electrical insulation
(Murray et al., 2000). Furthermore, production of
energy by lipid occurs only when the substrate is β-
oxidized with reduction of oxygen to water in the
respiratory chain. This process alone consumes 80
to 90% of the available oxygen while the rest is
used in non-enzymatic and direct chemical reaction
by oxidase and oxygenase enzymes in the body
(Gutteridge and Halliwell, 1999). Oxidation of
lipid without energy release which accompanies
the rancidity of un-saturated lipids as a result of
oxidative deterioration by reacting with molecular
oxygen is called lipid peroxidation (De Zwart et al.,
1999). This has long been a serious problem of fat
storage and as such a lot of studies have been
carried out on the subject. The process of lipid
peroxidation can be either enzymatic or non-
enzymatic. The latter occurs through the actions of
reactive oxygen species (ROS) like hydroxyl
radical, superoxide anion radical and hydrogen
peroxide. Moreover, nitric oxide and nitrogen
dioxide which are gaseous in nature can also cause
non-enzymatic lipid peroxidation. All these
radicals are produced as a result of partial reduction
of oxygen. Oxygen molecule is completely
harmless because it has two unpaired electrons in
its ground state with parallel spin. This now makes
it paramagnetic and consequently it cannot react
with organic molecules in the organisms except
when it is activated (Apel and Hirt, 2004). The
detection and measurement of free radicals are
difficult because of their intrinsic short life spans
(De Zwart et al., 1999). Despite the problem of
detection, electron spin resonance which has spin
trapping remains one of the few techniques that can
detect free radicals directly.

Seeking safety from damage and destruction
of free radicals at different sites has led to evolution
of sophisticated defence mechanism referred to as
anti-oxidative defence system (Gaté et al., 1999).
This comprises enzymatic and non-enzymatic
components for scavenging reactive oxygen
species. The scavenging process could be intracellular or extracellular depending on the location and formation of the antioxidant in question (Chaudiere and Ferrari−Iliou, 1999). Some examples of intracellular antioxidant enzymes are catalase, superoxide dismutase as well as glutathione peroxidase. The function of the antioxidant is to convert the highly reactive free radicals and reactive oxygen species to less reactive ones (Gaté et al., 1999).

In a normal condition, oxygen metabolites that are potentially toxic are produced in low concentrations. This leads to production of intercellular anti-oxidant and a balance is achieved to have healthy plants but when the concentration of the oxygen metabolites increases without corresponding increase in the concentration of the anti-oxidant enzymes, there will be induction of oxidative damage to protein, lipid and nucleic acid. To avoid this oxidative damage, there should be increase in the level of production of endogenous anti-oxidant defence in higher plants (Sharma et al., 2012). The problem posed by the free radicals and the reactive oxygen species (ROS) is called oxidative stress. This refers to imbalance between pro-oxidants and the antioxidants as a result of adverse environmental conditions and it results in potential damage because of increase in the level of intracellular ROS levels (Sharma et al., 2012). This could be the consequence of endogenous anti-oxidant depletion or increased formation of free radicals and other reactive species. The oxidative damage caused by these free radicals and their likes could be on DNA, lipids and proteins which can lead to dysfunction, disorganization and destruction of proteins, enzymes and ultimately the membranes because they are also made up of proteins and lipids (Halliwell, 1997). Oxidative stress can also impair membrane function, decrease fluidity, inactivate membrane-bound receptors as well as enzymes with increased permeability to ions which finally leads to membrane rupture (Gutteridge, 1995). If the oxidative stress is not checked until it becomes severe, it results in cell death (Dypbukt et al., 1994).

Tolerance to oxidative stress could be genetically controlled through the use of conventional breeding and transgene production. In the same vein, it could be physiologically circumvented through pre-sowing seed soaking treatment (seed priming). This technology has been proven to be effective in alleviating environmental stress problems (Wahid and Shabbir, 2005). This involves partial hydration of the seeds up to the point of germination to allow the biochemical activities of germination to occur without radicle protrusion (Sivritepe et al., 2005). Lipid peroxidation, which is an established yardstick for measuring the level of oxidative stress in rice plants, became less severe as a result of low malodialdehyde (MDA) concentration found in stressed plants that resulted from primed seeds (Goswami et al., 2013). As a result of low concentration of malondialdehyde produced in the stressed plants, there was low level of intracellular ROS as a result of seed priming treatment (Goswami et al., 2013). Furthermore, the use of brassinosteroids for seed priming led to increase in peroxidase, superoxide dismutase and catalase activities when Medicago sativa was subjected to salinity stress (Zhang et al., 2007). Also, salicylic acid priming of Vicia faba seeds resulted in increase in ascorbate peroxidase, glutathione reductase, catalase and peroxidase activities (Azooz, 2009) while similar success was achieved with Agropyrone longatum with the use of abscisic and gibberellic acid priming (Eisvand et al., 2010). Finally, hormonal priming of maize seeds was found to have led to acquisition of tolerance to abiotic stress through responsive and effective anti-oxidative system (Guan et al., 2009). From the ongoing, it could be summed up that priming technology is an effective means of combating oxidative stress and lipid peroxidation in plants. This does not mean that exceptions could not still be found in some other crops because the technology is still affected by plant types and varietal difference.

MECHANISM OF HOW SEED PRIMING WORKS

Knowing the mechanism of operation of priming works in seeds, succeeding seedlings and plants is sine qua non to appreciating the extolled success achieved by seed priming technology. Building of tolerance or resistance to stresses through pre-sowing treatment of seeds varies from
one plant to another and from one priming agent to another. The mechanisms used in different environments will now be examined in turns.

When cold becomes a constraint in plant production, transcription of genes plays multiple roles and expression of such genes also plays many roles in resistance pathway for biotic and abiotic stress in plant growth (Nguyen, 2009). Among the mechanisms used against cold stress when priming is employed is increase in levels of indole-acetic acid (IAA), abscisic acid (ABA) and gibberellic acid (GA$_3$) (Gharib and Hegazi, 2010).

As it is found in other environmental stresses, moisture stress also leads to biosynthesis of some enzymes or at worst increase or decrease in their activities. For instance, PEG priming of rice seeds led to higher activity of some enzymes like phenylalanine ammonia lyase (PAL), superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) than hydro-priming under moisture stress (Yuan−Yuan, 2010). In the same vein, moisture stress in primed rice seeds was physiologically alleviated by increasing the content of proline which is an osmo-regulating solute that confers stress tolerance on any plant when its concentration is above the threshold level (Atreya et al., 2009). Furthermore, there was increase in the level of soluble protein, reduction in malondialdehyde (MDA) concentration and promotion of glucose metabolism (Yuan−Yuan et al., 2010). These researchers further established that seedlings from primed rice seeds had increased activities of phenylalanine ammonia lyase, SOD, POD and CAT as enzymatic defence mechanism against moisture stress and decrease in malondialdehyde, soluble sugar and proline contents with increase in soluble protein content as physiological strategy against the stress.

Osmotic adjustment to tolerate saline environment through priming was demonstrated using salicylic acid for priming wheat seeds. This resulted in reduction of chlorophyll a and b contents as well as their ratio while there was increase in the concentration of soluble, reducing and non-reducing sugar in the leaves (Hamid et al., 2008). However, when kinetin and benzyl amine purine were used as priming media, there was increase in free salicylic acid and polyamines (Iqbal and Ashraf, 2006).

In flooded environments, better performance of plants through seed priming or hardening is engineered by biochemical changes like activation of enzymes and increase or decrease in their kinetics (Basra et al., 2005). These biochemical changes involve increase in amylase activity and reduction of sugar content (Farooq et al., 2010). Also, increase in soluble sugar content, proline level and total nitrogen content as well as decrease in concentration of insoluble sugar during germination (Mondal et al., 2011) are also parts of biochemical changes to withstand flood stress in rice.

**PRIMING IS A SOURCE OF STRESS TO SEEDS**

It has been categorically established that seed priming improves stress tolerance in plant from the previous discussion. Based on this fact, it is important to know whether seed priming constitute stress to primed seeds or not. It could be said that seed priming is a source of stress to the seeds based on the fact that it has been defined as a pre-germination exposure to stress which leaves the seeds with stress memory (Bruce et al., 2007) because it builds stress tolerance in some plants and they show stress responses (Chen et al., 2012). So, improved stress tolerance after germination is a manifestation of cross-tolerance induced by priming process (Chen and Arora, 2013). This tolerance could be built in different plants through different priming media. Inhibition of radicle protrusion in priming technology differentiates seed priming from normal germination and constitutes a source of stress to the treated seeds. It can, therefore, be said that priming is a form of stress imposition on seeds. For instance, PEG$_{6000}$ which is a routine agent of osmo-priming is used for triggering osmotic stress in different plants under laboratory conditions (Balestrazzi et al., 2011). Similarly, when sodium chloride was used for priming amaranth and sunflower seeds, the seeds were stressed through prevention of radicle protrusion. This restriction of radicle protrusion was not the result of toxicity of the solution used but that of osmotic stress of the solute used for preparing solution of non-toxic solution (Moosavi et al., 2009). In the same vein, if hydrogen peroxide
is used for priming, it will impose oxidative stress on the primed seeds because the priming chemical is a member of reactive oxygen species (ROS) (Chen and Arora, 2013). Furthermore, the use of drum priming exposed primed seeds to having imbibition below the required natural and that led to mild stress in them (Ashraf and Foolad, 2005). In addition to this, hydro-priming has been discovered to be stressful because it leaves imbibition injury and unavoidable ROS in the primed seeds (Bailly, 2004).

It is not only the priming media that imposes stress on the primed seeds but also the dry back that follows the treatment which gives the seeds opportunity of short-term storage before sowing. The reason for the stress was that priming procedure activates quiescent cellular activities in the primed seeds and that leads to desiccation tolerance (Yang et al., 2007). So, when seeds have been partially desiccated, such desiccation would constitute stress on them. The severity of the resulting injury varies according to the speed with which the drying is done and the extent to which the seeds lose their tolerance to desiccation. The speed of drying, slow or fast, can be deleterious to seedling vigour or cause lipid peroxidation (Chen and Arora, 2011). It could be concluded that priming process constitutes stress in the primed seeds while drying back makes the seeds experience some inevitable injury. So, the two processes are the sources of stress to the treated seeds and the resulting plants. The ability of the plants to tolerate stress after germination could be likened to vaccine given to animals to awake the defence system of their bodies so that disease could be fought effectively when it appears in reality.

**BIOCHEMICAL AND ENZYMATIC CHANGES RESULTING FROM SEED PRIMING**

Biochemical attributes of seeds and the resulting seedlings are normally modified when seeds are primed prior to sowing. The nature of their modification depends on types of plant, their species, priming chemicals, methodology used in priming and environmental conditions the resulting plants are subjected to. An instance of this was the use of ascorbic acid priming which increased total soluble sugar and phosphorus contents of wheat when it was grown under normal condition (Khan et al., 2011). As for activities of enzymes, increase or decrease in their activities is determined by biotic or abiotic stress from which the plant suffers. In cold stress for instance, salicylic acid (SA) priming induced cold stress tolerance by increasing polyphenol oxidase activities in cowpea (Gharib and Hegazi, 2010) and decreasing catalase (CAT) and peroxidase (POD) activities in beans (Gharib and Hegazi, 2010), maize (Bedi and Dhingra, 2008) and winter wheat plants (Tasgn et al., 2006). In the same vein, SA priming reduced over-production of hydrogen peroxide that accompanied CAT activities and that consequently led to enhancement of chilling tolerance in banana (Zhang et al., 2003) and matrela grass (Wang et al., 2009) by activating glutathione reductase and guaiacol peroxidase (Kang and Saltveit, 2002). Contrary to what happened in chilling stress tolerance, increase in CAT and POD activities through SA priming induced heat stress tolerance in kentucky blue grass (He et al., 2005).

**GENETIC EXPRESSION PATTERNS IN PRIMED SEEDS AND RESULTING PLANTS**

Determination of genetic basis associated with increase in germination and the subsequent better performance of the resulting plants from seed priming technology is of prime importance. Understanding this basis proffers solution to understanding the mechanism of seed priming effect on plants at different stages. In this direction, the use of quantitative trait locus (QTL) analysis using a recombinant inbred line (RIL) population revealed that QTL was responsible for 47% of the phenotypic variation that was evident as a result of priming technology (Schwember and Bradford, 2010). Similarly, the use of a low resolution mapping (LRM) showed that only a single significant QTL on linkage group (chromosome 6) could be identified and it was responsible for 39.3% of the variance that was conferred by the UC96US23 allele at that locus. This QTL also collocated with the one.
responsible for over 60% of the phenotypic variation in high temperature germination between the Htg6.1 parental lines (Agyris et al., 2008).

EFFECTS OF SEED PRIMING ON PROTEOMICS OF PRIMED SEEDS AND RESULTING PLANTS

Since seed priming is important in seed industry, there is a great need for characterization of specific protein markers for the improvement of the seed quality. This is of both economic and academic interests. During germination of hydro- and osmo-primed Arabidopsis for instance, there were three priming-associated polypeptides whose abundance increased as the priming process progressed and two of these intrinsic priming proteins were degradation products of 12S cruciferin β-subunits (Gallardo et al., 2001). This result was also observed when sugar beet seeds were primed (Job et al., 1997). The implication of this is that there are similarities in storage-protein mobilization among seeds of different families during priming process. However, it should be noted that seeds of different lots from the same cultivar and consignment can behave differently and thereby antagonistic or different results might become evident (Bassel et al., 2008). For instance, when tomato seeds from two seed lots were primed, they exhibited different responses despite being given the same treatments (Nkaune et al., 2012). This is not only found in molecular work but it is also found in biochemical, physiological and morphological studies. It has also been found that short-term priming with low salt concentration could lead to transcriptional enhancement of GA4 levels as well as SIGA2ox1, SIGA3ox1 and SIGA3ox2. Furthermore, such priming promoted expression of genes encoding cell wall modification enzymes which promoted micropyl endosperm cap weakening that resulted in uniform and higher germination percentage (Nkaune et al., 2012). It was added that despite the latest stages of research in this area, the mechanism by which priming solutions activate the expression of SIGA2ox1, SIGA3ox1 and SIGA3ox2 remained unclear and further elucidating research would be of high benefit.

Understanding biochemical and molecular mechanisms underlining seed vigour enhancement in relation to stress, protein and gene expression during seed germination could be achieved through studying a specific plant. In genomics and proteomics of Alfalfa (Medicago sativa) for instance, there were dynamic changes of 79 proteins which were responsible for protein metabolism, cell structure and defence during germination. Out of these proteins, 63 were specific to osmo-priming, 65 preferentially varied during germination while 14 were in their intersectional area (Yacoubi et al., 2011). It was further stated that there were detoxifying proteins which minimized cell damage because there was presumption that an oxidative stress that generated reactive oxygen species was initiated by osmo-priming. It is, therefore, concluded that priming is not only an advanced germination-related process but it also has germination improvement mechanisms like that of defence which empowers the seeds to overcome the obstructing environmental stresses that occur during germination.

DIRECT AND INDIRECT EFFECTS OF SEED PRIMING

It is a true fact that seed priming technology enhances germination, speeds up seedling emergence and improves seedling performance under normal and adverse growth conditions. This implies that seed priming has direct effects on primed seeds. In addition to that, if the priming process damages primed seeds, both seed germination and seedling production will be adversely affected. Success of seed priming is influenced by complex interaction of factors which include plant family, species, osmotic potential of the priming solution, duration of priming, ambient temperature, seed vigour and the storage condition of the primed seeds (Ghassemi-Golezani et al., 2010). For the effect priming on seeds, the study by Khan et al. (2011) revealed that hormonal and vitamin priming helped in better maintenance of seed cell wall and consequent preservation of seed leachates. This means that better membrane repair could be achieved using vitamin and hormonal priming. The repair occurs when seeds are soaked...
in osmotic solution and imbibition of water occurs until sensu stricto stage is reached without protrusion of the radicle (Bray, 1995). Physiological and biochemical changes that occur at the priming stage are directly carried on to the period of germination. These changes allow the treated seeds to move to the third stage of germination which involves radicle protrusion as soon as favourable environmental conditions are found. As for seeds that are not re-dried after priming treatment, a simple reduction in imbibition lag time aids speedy germination. Skipping of the first two stages of germination leads to achievement of speedy germination. This has been made evident when salicylate priming improved germination rate and seedling growth of fine and coarse rice (Farooq et al., 2007). Similarly, ascorbate and sodium salicylate priming improved germination rate and germination percentage of wheat (Al–hakimi and Amada (2001). All these results were attributed to metabolic repair during imbibition (Farooq et al., 2005), build- up of germination-enhancing metabolites (Basra et al., 2005) and osmotic adjustment (Farooq et al., 2005) during priming process. It should be, however, noted that seed priming does not make a non-viable seed viable but it only enhances the viable ones to fully express their potentials. The edge start of the primed seeds gives the resulting seedlings opportunities to develop extensive roots for quick absorption of water and nutrients which guarantee better plant establishment (Ghobadi et al., 2012). On the other hand, if the concentration of the priming solution is too high or duration of priming is too long, the germination is either retarded or hampered completely as a result of toxicity (Basra et al., 2005).

After the completion of germination and seedling establishment, direct effect of seed priming ceases. This is because seed priming causes metabolic changes like cell cycle related changes (De Castro et al., 2005), endosperm weakening by hydrolase activities (Bradford et al., 2000) and mobilization of storage proteins (Job et al., 2000) in germinating seeds only and not in the succeeding seedlings. Despite this fact, there is rapidity in growth and development of plants resulting from priming treatments. This achievement comes from better root development that occurs at germination and post germination stages. Through this development, roots absorb moisture and nutrients required for rapid growth and development. Through this, increase in leaf area accompanying growth of plant is also achieved. Leaf area increase leads to production of more photo-assimilate which is judiciously partitioned to the panicles during grain filling stage. In this way, increase in yield is actually achieved but it is not from direct effect of priming chemicals as it is found in germinating seeds. Alternatively, it could be said that improvement in grain yield per unit area indirectly results from having higher number of seedlings and better seedling establishment which are the direct benefits of seed priming (Ghasemi–Golezani et al., 2010).

Future trust

There is need for further investigation on the operational mechanism of osmotic and plant growth chemicals to understand the direction of their operation and how the chemicals can adversely affect treated seeds and succeeding seedlings or plants. In the same vein, conditions that will improve performance stability and consistence of results from priming technology should be investigated to save the technology from having only short-term claims in crop improvement. Moreover, optimum media concentration and priming duration for different crops should be established to bring ease to effective use of seed priming technology. Also, further investigation is required to determine the activities of other enzymes that are also involved in plant defence during stress (biotic or abiotic) to better understand the role of priming in alleviating plant stress. Finally, there are fluctuations and contradictions in some of the findings from priming technology, more research is further needed to stabilize the facts established on the technology.

Conclusion

It is clear that seed priming can improve yield and yield quality of different crops, aid direct seeding, confer tolerance on crops against drought,
salinity and low temperature stresses. It can also alleviate thermo-inhibition problem in seed germination as well as oxidative stress in growing crops. It is also clear that the wonders of seed priming are not magical because the mechanisms of its operations have been explained physiologically, biochemically and molecularly (using genomics and proteomics). Explanation of the happenings in both primed seeds and resulting plants has been given using enzymatic activities, gene expression and proteomics. It has also been made clear that seed priming has only indirect effects on plant while its direct effects are restricted to the treated seeds and resulting seedlings. However, seed priming does not generally guarantee improvement in all aspects of plant’s life and it can also lead to problems in the treated seeds or the resulting seedlings.

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