Review Article
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Reversal of age-induced seed deterioration through priming in vegetable crops – a review

Abstract

Vegetables play a vital role in human diet as well as in improving farm income. Good quality of seed is the basic input for success in vegetable production programme. However, age-induced seed deterioration of vegetable crops is an inexorable phenomenon which gets in the way of successful vegetable production. As such seed deterioration caused by ageing and its repair during early germination determine the success or failure of vegetable production system. Seed deterioration can be defined as the loss of quality, viability and vigour either due to ageing or effect of adverse environmental factors. While as ageing may be considered as progressive decline in biological functions accompanied by an increased risk of degenerative changes and death over time. The rate of deterioration rapidly increases with increase in seed moisture content, storage duration or temperature of storage. Loss of seed viability following ageing has been attributed to a series of metabolic defects that accumulate in embryonic and non-embryonic structures. At the cellular level, seed ageing is associated with various alterations including loss of membrane integrity, solute leakage, reduced energy metabolism, impairment of RNA (protein synthesis), and DNA degradation. Seed priming treatment i.e. slowly imbibing and then re-drying of seeds accomplished by soaking of seeds in a solution of low water potential, has been shown to reinvigourate the aged seeds. The reversal of ageing effects by seed priming has been explained by reduction of malondialdehyde (MDA) and free radicals production and maintenance of antioxidant activities due to DNA repair and favorable metabolic balance.

Keywords: ageing, seed deterioration, priming, metabolic repair, DNA, protein

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Introduction

Cultivation of vegetables is carried out in intensive production systems and success of this activity depends on the quality of seeds used. High physiological potential of seeds with rapid and uniform field emergence is a fundamental requisite for a good crop establishment, especially under adverse environmental conditions. Quality seed comprises those properties, which determine the potential for rapid uniform emergence and development of normal seedlings under a wide range of field conditions ASPB.[1] However, seed quality declines during field weathering, harvesting and/or storage Farhadi et al.,[2] unless special precautions are taken and the annual losses due to seed deterioration can be as much as 25% of the harvested crop. Seed deterioration may be defined as the loss of seed quality (viability and vigour) due ageing effects and adverse environmental factors particularly higher temperature, relative air humidity and oxygen/carbon dioxide ratio Kapoor et al,[3] Farhadi et al.[2] Jyoti et al.,[4] while the term seed vigour is used to describe the sum total of those physiological properties of the seed or seed lot which determine the ability to germinate and emerge rapidly in the soil particularly under adverse environmental factors Milosevic et al.[5] As seed deterioration increases, seed performance is progressively decreases. It is a serious problem particularly in developing countries where seeds are stored in places usually without a proper control of air humidity, temperature and O_2/CO_2 concentration.

Indeed seed deterioration due to ageing is an inexorable phenomenon and the best that can be done is to lower its rate Coolbear.[6] The possibility to regulate seed deteriorating environmental factors makes the basis for longer seed storage. Detrimental effects of ageing may also be nullified or even reversed (repaired) by exposing seeds to different priming treatments Tilden et al.,[7] Kibinza et al.,[8] Parmoon et al.,[9] which a controlled hydration technique where seeds are partly hydrated to allow metabolic events to occur without germination and are then re-dried to permit routine handling Heydecker et al.[10] Bradford.[11] Primed seeds usually have higher and synchronized germination (Farooq et al., 2009a) owing to simply a reduction in the lag time of imbibitions taking place McDonald;[12] Brock-lehurst et al.,[13] buildup of germination-enhancing metabolites Farooq et al.,[14] metabolic repair during imbibitions Burgass et al.,[5] Bray et al.[16] and osmotic adjustment Bradford.[11] Testing of seed viability using different seed vigour tests is of utmost important because vigour tests give results comparable to field germination particularly under unfavorable environmental conditions Milosevic et al.[5] Artificially induced ageing is a useful technique for lowering viability quickly for experimental purposes Rodo and Marcos-Filho, 2003. Accelerated ageing (AA) treatment involves exposing seeds to highly adverse storage conditions of high humidity and high temperature for specific periods of time. This test is able to provide information with a high degree of consistency and the biochemical changes during these artificial ageing conditions are assumed to be similar, if not identical, to those during natural ageing, and the difference being only the speed at which these changes occur. The present article reports a brief account of the effects of seed deterioration and priming on morpho-physiological and biochemical attributes of germinating seeds with special emphasis on vegetables.

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Seed deterioration and morpho-physiological attributes of germinating seeds

Seed deterioration is an undesirable and detrimental attribute of agriculture. As seeds age, they maintain germinability for some time but subsequently they enter a period of rapid decline in germination ability due to degenerative processes occurring inside the seed Kapoor et al.[17] As seed deterioration increases, seed performance is progressively decreases Jyoti et al.,[4] Artificial deterioration of onion seeds through AA treatments (100% R.H. and 45ºC temp.) showed a marked increase in seed moisture content (ranging from 11.8 to 24.0%) which was inversely proportional to the germination potential of seeds Powell.[18] Controlled deterioration (ageing) of pepper seed resulted in reduced germination percent (GP) but increased mean germination time (MGT) and the reduction in GP and the increase in MGT were proportional to their ageing duration Lanteri et al.[19] Decrease in seed vigour as affected by deterioration was also proven in mungbean Bishnoi et al.,[20] and chickpea seeds Dahiya et al.[21] Fabrizius et al.,[22] confirmed the possibility of predicting the actual germination rate of soybean seed during natural ageing by applying the AA test, the main factors being the time of natural ageing duration and degree of seed deterioration. Soybean seeds showed a rapid lose in vigour, viability and time taken to 50 per cent seed germination (T_{50}) due to AA treatment with 99.5% R.H. and 32±2°C temperature for 30days. Maity et al.[23] The rate at which the seed ageing process takes place depends on the ability of seed to resist degradation changes by protection mechanisms which are specific for each plant species Balesevic-Tubic.[24] Reports indicated that onion (*Allium cepa* L.) seeds exhibit very short life and lose their viability within 1-2 years Khan et al.[25]

Working on water melon and cucumber Demir et al.,[26] concluded that accelerated ageing of seeds at 45ºC significantly reduced the seed germinability in the laboratory. Kapoor et al.[17] reported that seed quality in chickpea cultivars deteriorated following AA treatment of 45°C and 100% humidity for 24, 48, or 72hours. With increasing time of ageing treatment, seed moisture content increased and all physiological parameters measured such as germination percentage, seedling root length, shoot length, and vigour index decreased in all varieties. Balesevic-Tubic et al.,[24] stated that accelerated ageing test can be used to predict the length of storage life of sunflower and soybean seed but soybean seed was more sensitive to damage and reduced germination during storage. Prolongation of AA period in rice seed led to deterioration of both germinability and seed viability Kapoor et al.[17] Artificially deteriorated seeds of chick pea in humid storage at 40°C for 0, 7, 14, 21 and 28days showed declined seed germination and growth in terms of radicle length, seedling length, root weight and seedling weight with increasing storage, and germination was zero after 21 or 28days Biabani et al.,[27] DeTunes et al.,[28] concluded that the use of unsaturated and saturated solutions of NaCl reduced water absorption by onion seeds as compared to plane water and suggested that 48 hour treatment was a better AA test for classification of the onion seed lots. Reduced seedling growth due to ageing is a consequence of decline in weight of mobilized seed reserve i.e. seed reserve depletion percentage Mohammadi et al.[29] AA ageing of sweet pepper seeds at 42ºC and 100% R.H. for 0, 5, 10, 15, 20, 25 and 30 days resulted in decreased germinability in terms of radical emergence (%) that was also differed significantly among different ageing duration Kaewnaree et al.[30] AA treatments also decreased GP, MDG, GI, germination uniformity (GU) and increased abnormal seedling (ABS) percentage Zahra et al.[31] Farhadi et al.;[2] Yadollhhi et al.,[32] Almeida et al.[33]

Seed deterioration and biochemical attributes of germinating seeds

Ageing is a progressive decline in biological function accompanied by an increased risk of degenerative disease and death over time. It is a complex and multifactorial process and there have been many theories proposed to explain this phenomenon at the molecular, cellular, systemic and evolutionary levels Weinert et al.,[34] Loss of seed germinability following natural ageing or controlled deterioration has been attributed to a series of metabolic defects Roberts[35] that is inability to synthesize RNA, proteins and damage to nuclear DNA Bray et al.,[36] Anderson.[37] Integrity of ribosomal RNA in seeds of *Allium porrum* has been found to correlate with germination performance Bray et al.,[16] Wood stock and Tylorson[38] explained that deterioration during accelerated ageing of soybean seeds involves an imbalance between glycolysis and tricarboxylic acid cycle (TCA). Studying with French bean seeds Cortelazzo et al.,[39] observed alterations in the arrangement of proteins, rupture of cell walls and decreased activity of acid phosphatase of aged seeds and suggested that enzymatic activity can be used as a bio-marker for seed viability and vigour. Kibinza et al.,[40] described that seed deterioration is associated with various cellular, metabolic and chemical alterations including chromosome aberrations and damage to the DNA, impairment of RNA and protein synthesis, changes in the enzymes and food reserves and loss of membrane integrity. Loycrajjou et al.,[41] established that ageing-induced-deterioration increased the extent of protein oxidation and thus induced loss of functional properties of proteins and enzymes.

Damage to the organization of cell membranes during seed ageing is an important factor in explaining seed deterioration Tilden et al.,[7] Senaratna et al.;[42] TeKrony et al.;[43] Ferguson et al.;[44] Grilli et al.;[45] Goel et al.[46] AA resulted in increased lipid peroxidation, decreased levels of antioxidants and reduced activity of several enzymes involved in scavenging of free radicals and peroxides Hsu et al.;[47] Bailly et al.;[48] Goel et al.[45] Working on AA of seeds Khan et al.,[25] showed that aged onion (*Allium cepa* L.) seeds exhibit increased electrolyte leakage while the leaching from un aged control seeds was observed as negligible. The loss of viability in seeds after ageing was appeared to relate with increased membrane destruction (loss of membrane integrity). Lipid peroxidation in terms of malondialdehyde (MDA) accumulation, auto-oxidation of lipids and increase in the content of free fatty acids throughout storage period has been reported as the main cause of initial biochemical changes resulting in seed damage during storage Balesevic-Tubic et al.;[49] Kibinza et al.[40]

Demirkaya et al.,[50] reported that onion seed viability during storage and drying declines with genotype specificity (Akgün-12, Valencia and TEG-502). They found that activities of antioxidant enzymes like catalase (CAT) and superoxide dismutase (SOD) were decreased in each cultivar due to seed ageing. Moreover, a high level of correlation was found between the loss of seed viability and the decreases that occurred in CAT and SOD activities, in the seeds. Free radical production, lipid peroxidation (oxidative damages of membrane) and enhanced free fatty acid levels are blamed to cause the deteriorative changes in seeds whereas free radical oxidation enzymic dehydrogenation and aldehyde oxidation of proteins might reasonably contribute to the progress of seed quality Ghassemi-Golezani et al.;[51] Shaban,[52] Free fatty acid can damage lipid bilayer particularly of mitochondria leading to reduced energy production and free radicals have potential to damage membrane, DNA, enzymes, protein and ultimately cellular repair mechanism Kapoor et al.;[17] Mahjabin et al.[53] Kaewnaree et al.,[30] performed an AA of sweet pepper seeds (42°C and 100% RH) and found that EC, K^+, Na^+, CA_2+ and Mg^{2+} concentrations were increased in soaked seed solution during 10-30days of ageing time. The decrease in germination ability was well correlated with increase in membrane deterioration as assayed by electrical conductivity and electrolyte leakage in soaked seeds. They further described that Malondialdehyde (MDA) was the major product of lipid peroxidation. Yadollhhi et al.,[32] showed that increasing ageing duration resulted in higher reduction in germination characteristics associated with decreased catalase(CAT) and ascorbate peroxidase(APX) activity. In order to safeguard the tissues through inhibition of the oxidative damage and detoxification, cells are equipped with various enzymatic and nonenzymatic compounds Kibinza et al.[8]

Seed priming and morpho-physiological attributes of germinating seeds

The main principle of seed priming is the control of water solution potential at low level Stuart et al.,[54] Seed priming has been successfully demonstrated to improve germination and emergence in many crops particularly seeds of vegetables and small seeded grasses Bradford.[14] Since the response to a given priming treatment can vary between crop species, the optimal priming treatment is determined by trial and error Bradford.[11] Priming of onion seeds by manitol (-1.1MPa) at 10°C for 8days resulted in reduced value of T_{50} (days taken to 50 per cent seed germination) by 46 per cent Furutani et al.[55] Odell et al.,[56] reported that tomato seeds primed with 1.5% K_3PO_4+1% KNO_3 solution at 35°C had germinated more rapidly as compared to unprimed seeds Alvarado et al. Bradford (1987) reported that osmotically primed tomato seeds showed improved stand establishment, early seedling growth and yield, and seedlings from primed seeds emerged earlier and more uniformly than seedlings from untreated seeds. Also, seedlings from primed seeds maintained greater mean plant dry weights, leaf areas and ground cover percentages than untreated seedlings throughout the pre-flowering period. In another experiment, it was found that salt solution priming of tomato seeds was more beneficial to subsequent germination than PEG solution (Haigh et al.,[57] Georghiou et al.[58] osmotically conditioned pepper seeds in 0.4M mannitol solution for 4 d retained a high rate of germination and germinated to a high final percentage as compared to untreated seeds.

Osmopriming of freshly harvested tomato *(Lycopersicon esculentum* Mill. cv. Moneymaker) seeds for 8 d in -1.0 MPa PEG-6000 solutions followed by drying (6% moisture) enhanced seed germination and improved seedling performance as compared with the untreated control Liu et al.,[59] They further stated that controlled hydration of seeds followed by drying (seed priming) is used to break dormancy, speed germination, and improve uniformity of radicle emergence. In another study, Cayuela et al.,[60] reported that priming of tomato seed with NaCl caused earlier emergence than non-primed seeds. Thay also reported that seed priming (150mM KNO_3 at 20°C for 4days) of tomato showed higher percentage germination than unprimed seeds at 15 or 20°C. McDonald[12] reported that sunflower seeds primed with osmotic solution of PEG-8000 improved the seedling length and dry mass of both shoot and root. Working on optimization of seed priming techniques in musk melon for improved germination ability and seedling growth Nascimento[61] found that an osmotic potential around -1.30MPa is most adequate in both aerated and non-aerated conditions. Osmopriming of fresh tomato seeds (Nagina, Pakit, Riogrande improved and Roma) with -1.1MPa aerated solution of Polyethylene glycol (PEG-8000), NaCI and KNO_3 for 24h. resulted in improved germination and seedling vigour by dormancy breakdown as compared with untreated seeds Farooq et al.[62] Osmopriming of asparagus (cv. Mary Washington cultivar) seeds at 25°C for seven or 14 days using PEG-6000 at-1.0 or -1.2MPa, or sea water at -3.3MPa; or for three days in distilled water presented higher germination speed, independently of their initial physiological quality Bittencourt et al.[63] Govinden-Soulange et al.,[64] reported that osmopriming with PEG at -1.25MPa for 2 days resulted in significantly higher germination percentage (79.1%) than untreated control seed (62%) of the tomato cv. Sirius. Besides, seeds primed for 2days emerged earlier than seeds primed for 7days.

Pereira et al.,[65] explained that priming of carrot seeds (cv. Brasília) in –1.0 and –1.2MPa PEG 6000 for four and eight days can be useful for improving carrot seedling emergence in the field and seed performance under supra and sub-optimal temperatures. Priming of parsley seeds with PEG 6000 and mannitol and revealed significant improvement in FGP against unprimed seed Dursun et a.,[66] Selvarani et al.,[67] reported that matric priming of onion seeds with sand for 24h in 80% WHC recorded the higher germinability over control as well as osmopriming or hydropriming treatments. However, in case of carrot the highest germination attributes were recorded with hydropriming (24h in water at double the volume of seed). An analysis of the available data across experiments carried out with different species under varying conditions showed an average 11% increase in percent germination and 36% shorter mean germination time (MGT) in primed vs unprimed seeds. Moreover, in primed seeds MGT was less dependent on temperature, which is consistent with the effects expected from the treatment Girolamo et al.,[68] Effectiveness of priming depends on concentration, duration and cultivar. Generally, priming had an effect on total germination percentage, mean germination time, germination index and the coefficient of velocity compared to control seeds Aloui et al.[69] Sori.[70] Seed priming studies on coriander Meriem et al.,[71] revealed that seed priming with NaCl had diminished the negative impact of salt stress in all cultivars and primed plants showed better response to salinity compared to unprimed plants. Maximum values were recorded in tolerant cultivar (Tunisian) whereas minimum values were noted in sensitive cultivar (Algerian). Zhang et al.,[72] investigated that seed priming with PEG increased the environmental range suitable for sorghum germination and has potential to provide more uniform and synchronous emergence.

Seed priming and biochemical attributes of germinating seed

The promotion of germination with seed priming may take place for several reasons, but completion of DNA repair during priming and onset of germination is associated with a rapid resumption of RNA and protein biosynthesis Osborne.[73] Priming of lettuce seeds (*Lactuca sativa* L. cv. Minetto) in aerated solutions of 1% K_3PO_4 and water at 15°C for various periods of time revealed that cell division occurred at 21h in water and at 27h in 1% K_3PO_4 prior to radicle protrusion Cantliffe et al.[74] Parallel observations have also been noted by Dell'Aquila et al.,[75] in wheat. A considerable enhancement in biochemical activity and germinability of leek seeds was observed during priming Bray et al.[16] Improved germinability of primed leek seeds was associated with marked increases in protein, DNA and nucleotide biosynthesis after a lag period of 6-12h following the end of the priming period Bray et al.[16] Pepper seeds primed in NaCl solutions of -0.90 and -1.35MPa for 12days recorded an increase in soluble protein content by 109 and 120%, respectively Smith et al.[76] Davison et al.,[77] observed that five polypeptides were synthesized in the embryonic tissue of leek seeds after priming in -1.0MPa PEG solution. Lanteri et al.,[78] found that osmopriming of pepper and tomato seed in -1.1, -1.3, and -1.5MPa PEG for 14days reduced the mean time of germination because two amino acids were incorporated in proteins during the first 24h of imbibition of sweet pepper seeds in PEG solution Khan.[79] The positive effects of priming on the germination performance of many species are attributed to the induction of biochemical mechanisms of cell repair: the resumption of metabolic activity can restore cellular integrity, through the synthesis of nucleic acids (DNA and RNA), proteins and the improvement of the antioxidant defense system Bewley et al.[80] Improvement in germination of watermelon seeds by priming might also be due to enhanced repair of membrane and reduced leakage of electrolytes Chiu et al.[81] Osmopriming of pepper seeds in PEG Lanteri et al.,[82] might have induced DNA replication in the embryo root tips.

Primed sunflower seeds diverted a greater part of the cotyledonary resources towards the shoot which was crucial to its earlier establishment and photosynthesis for vigourous growth. It also reprogrammed the gene expression leading to *de novo* protein synthesis, a membrane repair mechanism and other substrates available for improved and synchronized germination Cruz-Garcia et al.[83] Improved germinability of tomato seeds due to osmopriming with PEG or K_2HPO_4 was associated with increased Catalase (CAT) and Peroxidase (POD) enzymes and decreased Malondialdehyde (MDA) concentration El-Araby et al.[84] Farooq et al.,[62] stated that osmopriming of tomato seeds resulted in lower electrical conductivity of seed leachates than untreated seeds. Priming of tomato seeds with KNO_3 decreased the level of MDA and increased the amount of chlorophyll in leaves Theerakulpisut et al.,[85] Zhang et al.,[86] reported that osmopriming (PEG-10% for two days) of tomato seeds improved the germinability and declined in the relative electrolyte leakage (REL) and in malondialdehyde (MDA) during the imbibition stage. Seed priming also brought about a considerable increase in biochemical parameters *viz*., chlorophyll a and b, total chlorophyll and carotenoids contents Kalpana et al.;[87] Zhang et al.;[72] Mirlotfi et al.[88]

Reversal of seed deterioration through priming – morpho-physiological attributes

Accelerated ageing predisposed seeds to imbibition injury. Germinability of accelerated aged seeds (50 hours) was increased from 10 to 90% by controlling the rate of imbibitions Tilden;[89] Tilden and West,[7] A reversal of seed germinability and seedling growth in lettuce seeds lost due to ageing was reported by Rao et al.[90] Bray et al.,[16] found that osmopriming treatments reduced both the mean time to germination and the spread of germination for two leek seed-lots of high viability but differing vigour. In addition, the differences in germination performance between these two seed-lots, was abolished by the priming treatments. Bailly et al.,[48] explained that the effect of priming in sunflower seeds was found to help the previously aged seeds to regain their initial ability. Reversal of seed deterioration by priming generally occurs in the meristematic axis or the radical tip Fu et al.,[91]

Delayed effect of controlled seed deterioration on seed germination in cauliflower has been found to lighten by exposing the seeds to osmopriming treatments Fujikura et al.[92] Basra et al.,[93] reported that osmotic priming of aged onion seeds with 25% PEG-8000 for 5days resulted in a marked increase in the rate of germination and early seedling growth. McDonald[94] concluded that artificial ageing of tomato seeds increased the percentage of aberrant anaphases in seedling root tips while osmopriming partially counteracts the detrimental effects of artificial ageing on germination rate, uniformity and normal seedling; however, it did not influenced the frequency of aberrant anaphases in seedling root tips. Kausar et al.,[95] reported that priming of low vigour seeds in sunflower hybrids was found effective in reducing the time for 50% germination and mean germination time (MGT) with increase in germination percentage. Many seed priming treatments have been used to reduce the damage of ageing and invigourate their performance in several crops Farooq et al.[96] Seeds of sunflower (*Helianthus annuus* L.) were aged at 35°C for different durations and then primed by incubation for 7 days at 15°C in a solution of PEG-8000 (-2MPa). The deprived germination potential due to ageing was found to revive in osmoprimed seeds Kibinza et al.[8] Ghassemi-Golezani et al.,[97] reported that hydro-priming of aged chickpea seeds repaired seed deterioration and enhanced their performance in the field.

Siadat et al.,[98] reported that increasing ageing duration in maize (*Zea maize* L.) seeds resulted in higher reduction in germination characteristics. Seed priming with KNO_3 had positive effects on seed germination of aged seed. Zhang et al.,[85] found that osmopriming (PEG-10% for two days in dark) of aged tomato (ZZ1 hybrid) seeds had enhanced germination percentage (GP), germination index (GI) and mean germination rate (MGR) with a substantial increase in the radicle length (RL), shoot length (SL) and total fresh weight (FW) compared with unprimed aged seeds. Parmoon et al.,[9] found that accelerated ageing of milk thistle seeds reduced the germination rate and seedling growth while as osmopriming treatments induced perking up of germination percentage, seed vigour and seedling growth. Priming of aged French bean (*Phaseolus vulgaris* L.) seed improved the seed quality and showed improved seedling length, seedling dry weight which in turn improved higher seedling vigour index, germination speed and mean germination time Sarika et al.[99] Kanwar et al.,[100] subjected the bitter gourd (*Momordica charantia* L.) seeds (cv. Solan Hara) to accelerated ageing (AA) and found that AA reduced the seed quality parameters in terms of germination percentage, seedling length, dry weight and vigour index I and vigour index II while as osmopriming of healthy as well as aged seeds was found to improve germination behavior.

An increased activity of antioxidant enzymes like Ascorbate peroxidases (APX), catalase (CAT), peroxidase (POX/POD) and superoxide dismutase (SOD) as a consequence of seed priming has been reported in various crops which have been attributed to protection against oxidative damage caused by seed accelerated ageing and salinity in nutrient solutions De Oliveira et al.;[101] Zhang et al.[72] Tilden and West[7] notified that slow hydration of germinating seeds prevented seed electrolyte leakage which indicates that cell membrane permeability or rupture was a major factor contributing to the loss of germinability after ageing. The mechanism of this reversal was considered as metabolic repair which probably included other sub-cellular components as well as the plasma membrane. Rao et al.,[90] observed a reversal of chromosomal damage (induced during seed ageing) with partial hydration of lettuce seeds by osmopriming to 33 to 44%. Reversal of deteriorated seed by priming generally occurs in the meristematic axis or the radicle tip Fu et al.,[91] Fujikura Karssen[92] reported that germination and initiation of incorporation of S-methionine into radicle tips of cauliflower were delayed by controlled deterioration which was accelerated by osmopriming of seeds. There were proteins whose expression was correlated with the rate of germination, and was reduced by controlled deterioration but enhanced by osmopriming. Basra et al.,[93] reported that osmotic priming of aged onion seeds with 25% PEG-8000 for 5 d resulted in a marked reduction of electrolyte leakage as well as lipid peroxidation and increased levels of antioxidants (ascorbic acid & tocopherols and catalase & peroxidase) involved in the mitigation of oxidative damage. Controlled humidification of aged pea seeds (priming) to 16.3-18.1% just prior to sowing was found to decreased chromosomal aberration, reduced imbibitional injury and improved seed viability Sivritepe et al.[102]

Bray[103] stated that priming is responsible to repair the age related cellular and sub-cellular damage of low vigour seeds that may accumulate during seed development. Lanteri et al.,[19] reported that effects of ageing pepper (*Capsicum annuum* L.) seeds may be partly reversed by priming and part of priming effects is related to the induction of nuclear replication. The induction of DNA replication in aged seeds may thus serve as an indicator for the resumption of metabolic activities in the seed during imbibition in water or PEG. Taylor et al.,[104] described that seed priming can reverse some of the ageing-induced deteriorative events (changes in enzymatic activities and decline in protein and nucleic acid synthesis and lesions in DNA) and thus improve seed performance. Priming appears to reverse the detrimental effects of seed deterioration by increasing the free radical scavenging enzymes and counteracting the effects of lipid peroxidation and reduce leakage of metabolites Bailly et al.;[48] McDonald.[12] According to Gonzalez-Zertuche et al.,[105] priming of *Wigandia urens* aged seeds showed increased protein concentration and also induced the synthesis of heat stable proteins of 14 and 23kDa in aged seeds and proteins of high molecular weight of 43 kDa in primed seeds that were not detected in control seeds. Kibinza et al.,[8] informed that accelerated ageing affected seed germination and priming treatment reversed partially the ageing effect. The inhibition of catalase by the addition of aminotriazol during priming treatment reduced seed repair indicating that catalase plays a key role in protection and repair systems during ageing. These results clearly indicate that priming induce the synthesis of catalase which is involved in seed recovery during priming. Increased seed deterioration due to ageing has been reported to associated with increased lipid peroxidation, free radical increment and decrease antioxidants activity while as improved seed repair and germinability due to seed priming was found to associated with increased catalase and peroxidase activity Siadat et al.;[98] Parmoon et al.[9]

Siri et al.,[106] reported that osmopriming (PEG-6000 with -1.5MPa for 6days) of artificially aged seeds of sweet pepper (42oC and 100%RH) resulted in an improved germination with decreased levels of malondialdehyde (MDA) and total peroxide concentration. They further stated that accumulation of total antioxidant activity (TAA), total ascorbate, dehydroascobate and catalase (CAT) activity in primed seeds enhanced the defense mechanism in protecting the cell membrane damage from reactive oxygen species. Working with bitter gourd (*Momordica charantia* L.) seeds Kanwar et al.,[100] reported that improvement in germination attributes of healthy and aged seeds due to seed priming was mediated through initiation of cell cycle, metabolic repair and reduction in the deleterious effects of ageing. Krainart et al.,[107] informed that priming of aged cucumber (*Cucumis sativa* L.) seeds using $KH_2PO_4$and PEG 6000 (-1.0MPa) at 15°C for 72 hours improved the quality of seeds through reduced amount of Malondialdehyde and total peroxide and increased antioxidant activity.

Conclusion

Seed deterioration due to ageing is a natural and inexorable phenomenon which is regulated by various metabolic activities especially related to protein and lipid metabolism as well as the generation of free radicals and antioxidant system present in the seed. However, rate of deterioration can be slowed down up to a significant level by manipulating the environment (Temp. humidity and O_2/CO_2) around the seed. Seed priming is a wonderful technique of seed invigoration which has the potential not only to enhance the seed vigour and germinability of normal seeds but also has the excellent ability to revive the partially aged seeds and improve the germination power over a wide range of environmental conditions.

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Conflict of interest

The author declares no conflict of interest.

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