Indian Journal of Agricultural Sciences **95** (9): 1108–1113, September 2025/Article
https://doi.org/10.56093/ijas.v95i9.158482

Effect of natural ageing on physiological and biochemical behaviour of onion (*Allium cepa*) seeds having differential initial seed quality

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Received: 20 October 2024; Accepted: 25 July 2025

ABSTRACT

Onion (*Allium cepa* L.) seeds are short-lived and the seed quality deteriorates during storage. The understanding of seed deterioration associated with the ROS content along with the antioxidant enzyme activities specifically in relation with initial seed germination potential is not available. A study was carried out during 2022 and 2023 at ICAR-Indian Agricultural Research Institute, New Delhi to assess the biochemical behaviour of onion seeds having differential initial germination percentage, under ambient storage condition. Freshly harvested seeds of four onion genotypes i.e. Sukhsagar, POS 24K, Bhima Super and Bhima Shubhra, having different initial seed germination percentage ranging from 84–96 % were stored under ambient conditions for 12 months. The seed germination declined, ranging from 49–77 % after 12 months with a percent decline in germination ranging from 19–46%. An increase in the activity of NADPH oxidase, ROS as well as malondialdehyde content and decline in antioxidant enzyme activity was observed in onion seeds after storage. A significant positive correlation was found among germination percentage, catalase, peroxidase and superoxide dismutase activity, whereas germination percentage was negatively correlated with superoxide radical, hydrogen peroxide, MDA content and NADPH oxidase activity. The study implicated the critical role of catalase, peroxidase and superoxide dismutase in ameliorating the negative impact of superoxide radical, hydrogen peroxide that causes deterioration with seed ageing without being affected by initial germination potential.

Keywords: *Allium cepa* L., Antioxidant enzymes, Lipid peroxidation NADPH oxidase, Natural ageing, Reactive oxygen species

Onion (*Allium cepa* L.) is one of the important commercial vegetable crops with significant nutritional and economic value belonging to the family Amaryllidaceae. At the global level, India is the second largest producer of onion, after China with a production of 31.27 million tonnes (MoA and FW 2022). Onion seeds are typically stored for extended periods, undergoing various physiological and biochemical changes thus affecting their viability and vigour. Temperature and relative humidity during storage significantly influence the storability. Besides, other seed deteriorating factor includes higher lipid peroxidation due to their high lipid content (22–26%) and a fragile seed coat prone to cracking at the hilum, which promotes fungal infections (Mohamed-Yasseen *et al*. 1996, Hornke *et al*. 2020).

During storage, a decline in germination and seedling development occurs due to irreversible degenerative changes in the seed, including loss of membrane integrity, physical damage, impaired enzymatic and metabolic activities, alterations in composition and cellular structure and overall quantitative losses (Balikai *et al*. 2019). Antioxidant enzymes, such as Catalase (CAT), Peroxidase (POX) and Superoxide dismutase (SOD), play a crucial role in mitigating the deleterious effect of Reactive oxygen species (ROS). These enzymes help to maintain cellular redox homeostasis and protect seed viability during storage. The physiological and metabolic state of seeds during storage impact the ROS production (Foyer *et al*. 2017, Zhang *et al*. 2021). Highly reactive forms such as lipid hydroperoxides are produced during lipid catabolism producing malondialdehyde (MDA) as their byproduct (Ayala *et al*. 2014). Lipid peroxidation not only destroys lipids, but it also causes extensive damage to cell membranes. Understanding the metabolic changes during oxidative stress caused by ROS is crucial to enhance the information of cellular resilience and seed ageing, providing broader implications for seed longevity.

Researchers (Demirkaya *et al*. 2010, Kamaei *et al*. 2024) have found a substantial link between loss of seed viability and catalase and superoxide dismutase enzyme activity in onion seeds but the complete understanding of

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onion seed deterioration is not available. The association of initial seed germination potential with the changes in ROS generating NADPH oxidases, ROS content, and MDA content along with the catalase, peroxidase and superoxide dismutase enzyme activities is not available for onion seed stored under ambient condition. Reviewing this research gap, we aim to investigate the changes in physiological and biochemical behaviour in onion seeds stored under ambient condition, with respect to their initial germination potential. By elucidating the relationships between these factors, we seek to provide insights into the mechanism of seed deterioration and identify potential strategies for improving seed quality after storage.

MATERIALS AND METHODS

Plant materials and experimental design: A study was carried out during 2022 and 2023 at ICAR-Indian Agricultural Research Institute, New Delhi. The freshly harvested seeds of onion genotypes, Sukhsagar and POS 24K were collected from ICAR-Indian Agricultural Research Institute, New Delhi, whereas Bhima Super and Bhima Shubhra were procured from ICAR-Directorate of Onion and Garlic Research, Pune. The seeds were equilibrated to 7–8 % moisture content by conditioning in desiccator for a period of three days, followed by storage in cloth bags under ambient temperature and relative humidity condition for 12 months (Supplementary Table 1). The seed germination was assessed in accordance with International Seed Testing Association's guidelines at 0, 6 and 12 months of natural ageing. Four replicates of 50 sterilized seeds were placed in petri plates in a germination chamber maintained at 20°C and 100% RH. Following twelve days, Germination Percentage (GP) was scored based on the counting of normal seedlings and calculated as:

GP = Number of normal seedlings × 100/Total number of seeds

Seed quality evaluation was done under laboratory conditions at ICAR-Indian Agricultural Research Institute, New Delhi. Descriptive statistics, including mean ± SD values, were analysed using the ANOVA test, accompanied by a Tukey's HSD test using IBM SPSS software. Pearson's correlation test and Principal Component Analysis (PCA) were analysed using The Jamovi Project (2020) (version 1.6).

Biochemical analysis: The biochemical analysis was done using standard protocols for NADPH oxidase (Van Gestelen *et al*. 1997), superoxide radical (Chaitanya and Naithani 1994), Hydrogen peroxide (Rao *et al*. 1996), malondialdehyde content (Heath and Packer 1968), superoxide dismutase (Beauchamp and Fridovich 1971), catalase (Aebi 1984) and peroxidase (Chance and Maehly 1955), was undertaken at ICAR-Indian Agricultural Research Institute, New Delhi, at 0, 6 and 12 months ageing of stored seeds.

RESULTS AND DISCUSSION

Several studies on onion seeds have reported significant variability for seed longevity (Hornke *et al*. 2020, Pal *et al*. 2023, Kamaei *et al*. 2024). Maintaining a high germination percentage of onion seeds (i.e. 70% as per Indian Minimum Seed Certification Standards) is difficult due to rapid deterioration during storage. The control (unaged) seeds of onion genotypes had a variable initial germination percentage, 84% in Sukhsagar and POS 24K whereas, 96% and 95% (statistically at par) in Bhima Super and Bhima Shubhra (Table 1). After ageing of 12 months, Bhima Super has the highest Germination Percentage (GP) (77%, above IMSCS), followed by Sukhsagar (65%), POS 24K (51%) and Bhima Shubhra (49%). The highest decline in GP after 12 months storage was observed in Bhima Shubhra (46%) and POS 24K (33%) whereas the lowest decline was reported in Bhima Super (19%) and Sukhsagar (19%). The above results concluded that Bhima Super is a good storer as it retained GP above IMSCS even after 12 months of ageing, followed by Sukhsagar which showed reduction in GP below IMSCS after 6 months ageing (Fig. 1). While POS 24K and Bhima Shubhra were poor storers as GP declined below IMSCS within 6 months of ageing. Initial seed quality has not played role in seed storability as the genotypes with similar GP at 0 months i.e. Sukhsagar and POS 24K (84%) showed differential seed storability behaviour. Despite the low initial GP, Sukhsagar retained the GP above IMSCS after 6 months, to classify Sukhsagar as a better storer. Bhima Super and Bhima Shubhra having high initial GP (96 and 95%, statistically at par) behaved differently after 6 as well as 12 months of storage and hence are classified as good and poor storers, respectively (Fig. 2). Similar results on a significant loss of viability during ageing have been reported (Brar *et al*. 2019, Balikai *et al.* 2019, Zhang *et al*. 2021, Pal *et al*. 2023).

Reactive Oxygen Species (ROS) are byproducts of plant metabolism, primarily generated in specific cellular compartments and through enzymatic and non-enzymatic reactions in seeds during storage (Foyer *et al*. 2017). The NADPH oxidase enzyme plays a key role in ROS production in seeds, generating superoxide radicals ($O_2^{\bullet-}$) that is also converted to hydrogen peroxide (H_2O_2) and highly reactive hydroxyl radicals ($OH^{\bullet}$) (Ishibashi *et al.* 2015). In our study, after 6 months of ageing, significant increase in NADPH oxidase activity was observed in all genotypes. At 12 months of ageing, NADPH oxidase activity significantly increased in Sukhsagar (0.68 µmol/g FW seed/min), POS 24K (1.03 µmol/g FW seed/min), Bhima Super (0.61 µmol/g FW seed/min) and Bhima Shubhra (0.92 µmol/g FW seed/min) where highest increase over unaged seeds was observed in POS 24K (136%) and lowest in Bhima Super (56%) (Table 2). Superoxide radical is a reduced form of oxygen molecule (unpaired electron) and its generation is catalyzed by the NADPH oxidase enzyme. After 6 months of ageing, highest increase (95%) in superoxide content was recorded in POS 24K (13.08 µmol/g FW) as compared to unaged seeds. Whereas, at 12 months of ageing, Bhima Shubhra (14.61 µmol/g FW) recorded highest increase (152%) in the superoxide content but Sukhsagar (10.34 µmol/g FW) exhibited lowest increase (89%) among all the onion

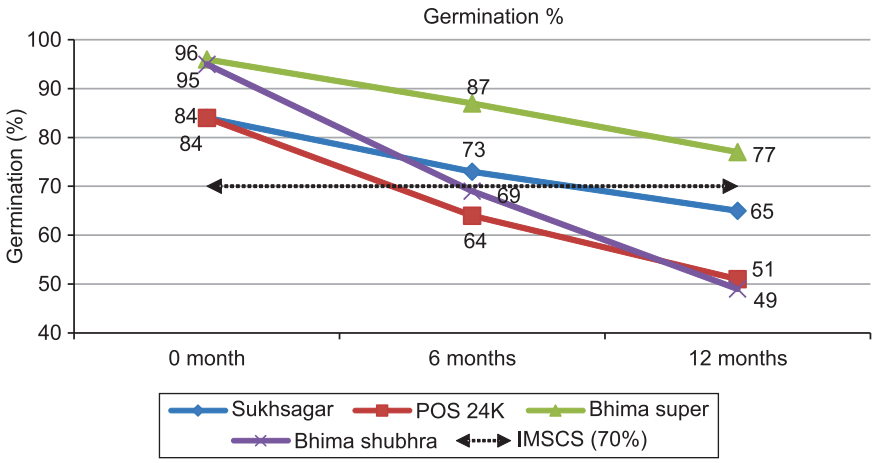

Fig. 1 Germination percentage at 0, 6 and 12 months of natural ageing in onion genotypes. IMSCS, Indian Minimum Seed Certification Standards.

genotypes (Table 3). In the current study, the hydrogen peroxide content of unaged seeds of the onion genotypes were almost similar (4.65, 4.92, 4.39 and 4.51 µmol/g FW). The H_2O_2 content in 12-month aged seeds of POS 24K and Bhima Shubhra increased by 80 and 86% whereas Sukhsagar and Bhima Super recorded 47 and 54% increase in H_2O_2 content over unaged seeds (Table 3). The aged seeds produced higher levels of $O_2^{\bullet-}$ and H_2O_2 as compared to unaged seeds. Among the genotypes, Sukhsagar and Bhima Super showed an increase in ROS content although it was significantly lower than POS 24K and Bhima Shubhra. The rate of ROS production during first 6 months (0 to 6 M) was higher as compared to later 6 months duration (6 to 12 M) which correspond to decline in GP in the respective genotypes; higher the rate of ROS production, higher is the decline in GP during ageing (Fig. 2). The higher ROS production rate in poor storers led to higher decline in GP, irrespective of the initial GP. An increase in the NADPH oxidase activity with the progression in storage period has contributed in accumulation of ROS. The higher $O_2^{\bullet-}$ and H_2O_2 accumulation in aged seeds was associated to the increased activity of NADPH oxidases, which was in conformity with the results of Ishibashi *et al*. (2015) and Kumar (2020).

Lipid peroxidation is a ROS mediated oxidative degradation of lipids leading to increased cytotoxic lipid hydroperoxides and aldehydes in the cells. In the present study, the MDA content of all the onion genotypes increased with ageing (Supplementary Table 2). After 6 months of ageing, MDA content in Bhima Super (23%), Sukhsagar (26%), POS 24K (39%) and Bhima Shubhra (48%) increased significantly as compared to unaged seeds. With ageing of 12 months, MDA content in all genotypes increased significantly. The poor storer genotypes recorded a higher increase in MDA content as compared to good storers post ageing with a higher rate of MDA production in the initial 6 months storage. Seed ageing in onion is a result of a slowing down in synthesis processes, which may be attributed to protein degradation, enzyme inactivation and increased lipid peroxidation during seed ageing (Ayala *et al*. 2014, Kumar 2020).

Table 2 Effect of natural ageing on NADPH oxidase activity in different genotypes

	NADPH oxidase activity (µmol/g FW/min)		
Ageing/ Genotype	0 month	6 months	12 months
Sukhsagar	0.42^{ab}	0.58^{c} (38)	0.68^{c} (62)
POS 24K	0.44^{a}	0.84^{a} (93)	1.03^{a} (136)
Bhima Super	0.39^{b}	0.52^{d} (33)	0.61^{d} (56)
Bhima Shubhra	0.43^{a}	0.74^{b} (72)	0.92^{b} (113)
CD (p<0.05)	Ageing: 0.029	Genotype: 0.034	A×G: 0.059
SEM±	Ageing: 0.010	Genotype: 0.012	A×G: 0.020

Letters in superscript indicate significant differences at p<0.05 using the LSD tests; Values in parentheses are percent change in values with ageing over fresh seeds (0 month); A×G, Ageing × Genotype.

Table 1 Effect of natural ageing on germination percentage and percent decline in germination in different genotypes

	Germination percentage (%)			Decline in germination percentage with ageing	
Ageing/ Genotype	0 month	6 months	12 months	6 months	12 months
Sukhsagar	84^{b} (66.4)	73^{b*} (58.7)	65^{b} (53.7)	11	19
POS 24K	84^{b} (66.4)	64^{d} (53.1)	51^{c} (45.6)	20	33
Bhima Super	96^{a} (78.4)	87^{a*} (68.9)	77^{a**} (61.3)	9	19
Bhima Shubhra	95^{a} (77.1)	69^{c} (56.1)	49^{c} (44.4)	26	46
CD (p<0.05)	Ageing: 1.41		Genotype: 1.63	Ageing × Genotype: 2.82	
SEM±	Ageing: 0.45		Genotype: 0.52	Ageing × Genotype: 0.91	

* indicates GP above IMSCS at 6 months; ** indicates GP above IMSCS at 12 months of natural ageing; Letters in superscript indicate significant differences at p<0.05 using the LSD tests; Values in parentheses are transformed values.

SOD is an antioxidant enzyme involved in catalyzing dismutation of superoxide radical into O_2 and H_2O_2. With 6 months of ageing, Sukhsagar, POS 24K, Bhima Super and Bhima Shubhra showed significant decrease in the SOD activity (2.48, 2.01, 2.34 and 1.91 units/g FW seed, respectively). The SOD activity further decreased after 12 months of ageing with highest decrease in SOD activity in case of Bhima Shubhra (60%) whereas lowest decrease in Sukhsagar (40%) over fresh seeds (Supplementary Table 2). Second one being the CAT activity in unaged seeds of Sukhsagar, POS 24K, Bhima Super and Bhima Shubhra was recorded (2.12, 2.02, 2.20 and 2.12 µmol H_2O_2/g FW/min, respectively). After 6 months of natural ageing, a decreased CAT activity was recorded in the genotypes whereas, the CAT activity further decreased with 12 months of ageing to 40, 46, 58 and 64% of initial CAT activity in Sukhsagar, Bhima Super, POS 24K and Bhima Shubhra (1.27, 1.18, 0.85 and 0.76 µmol H_2O_2/g FW/min, respectively) (Supplementary Table 3). Third one being the POX activity, the unaged seeds of Sukhsagar, Bhima Super and Bhima Shubhra were statistically at par whereas POS 24K recorded significantly lower POX activity (0.65 µmol/g FW/min). After 6 months of ageing, all the genotypes recorded significantly decreased activity of peroxidase (0.53, 0.39, 0.53 and 0.40 µmol/g FW/min) as compared to unaged seeds. With ageing of 12 months, the peroxidase activity further decreased in Sukhsagar (42%), POS 24K (66%), Bhima Super (35%) and Bhima Shubhra (59%) as compared to unaged seeds (Supplementary Table 3). The results of our study comply with decreased antioxidant enzyme activity found by Kamaei *et al*. (2024).

Similar results were also obtained with correlation matrix, where all the studied correlations were highly significant at p=0.01 with high absolute values. All the biochemical parameters were highly correlated with GP where CAT, POX and SOD were positively correlated while H_2O_2, $O_2^{\bullet-}$, MDA and NADPH oxidase were negatively correlated with GP. The high positive correlation between GP and antioxidant enzymes showed that the reduced germination of seed after natural ageing might be caused by reduced antioxidant enzyme activity. It is well known that ROS (H_2O_2 and $O_2^{\bullet-}$) are produced due to higher activity of NADPH oxidase, causing higher lipid peroxidation (higher MDA) resulting in seed deterioration and the same was observed by a highly positive correlation between H_2O_2, $O_2^{\bullet-}$, MDA and NADPH oxidase with each other (Supplementary Fig. 1) and the similar outcome was established by Kumar (2020) and Zhang *et al*. (2021).

Summarising the results, all the genotypes have recorded a decrease in the antioxidant enzyme activity (SOD, CAT and POX) with a comparatively higher rate of decrease in poor storer genotypes, after 6 and 12 months of storage (Fig. 2) (Supplementary Table 4). Moreover, the genotypes having higher rate of decrease in the antioxidant enzymes activity in aged seeds were also having comparatively poor GP after ageing irrespective of the initial GP. The decreased antioxidant activity caused seed deterioration due to higher accumulation of the ROS in POS 24K and Bhima Shubhra genotypes leading to their poor germination. Similarly, studies on various vegetable crops including onion, have reported declining CAT, POX and SOD activities with increased ROS during seed ageing, indicating a consistent pattern of antioxidant enzyme changes during ageing (Brar *et al*. 2019, Kamaei *et al*. 2024). However, the interrelation of ROS and antioxidant enzymes with genotypes having differential initial germination percentage is the novelty of our study and has not been studied so far.

Fig. 2 Descriptive model diagram showing interrelation between seed germination percentage and rate of decrease in antioxidant enzyme activity, rate of ROS production, rate of NADPH oxidase and rate of MDA production (per day).
GP, Germination Percentage; M, Months; Values shown in boxes are percent decline in germination percentage with ageing, over fresh seeds (0 month).

The present study unveils the impact of natural ageing on seed physiology and biochemical behaviour, and concluded that the seed germination declined, irrespective of the initial seed quality with ageing due to seed deterioration. The genotypes have been

Table 3 Effect of natural ageing on superoxide radical and hydrogen peroxide content in different genotypes

Superoxide radical (µmol/g FW)				Hydrogen peroxide (µmol/g FW)			
Ageing/ Genotype	0 month	6 months	12 months	Ageing/ Genotype	0 month	6 months	12 months
Sukhsagar	5.48^{b}	8.47^{c} (55)	10.34^{c} (89)	Sukhsagar	4.65^{ab}	6.34^{c} (36)	6.83^{c} (47)
POS 24K	6.71^{a}	13.08^{a} (95)	16.44^{a} (145)	POS 24K	4.92^{a}	8.00^{a} (63)	8.84^{a} (80)
Bhima Super	5.33^{b}	8.11^{c} (52)	10.38^{c} (95)	Bhima Super	4.39^{b}	6.09^{c} (39)	6.75^{c} (54)
Bhima Shubhra	5.81^{b}	11.02^{b} (90)	14.61^{b} (152)	Bhima Shubhra	4.51^{b}	7.60^{b} (68)	8.39^{b} (86)
CD (p<0.05) =	Ageing: 0.449	Genotype: 0.518	A×G: 0.898	CD (p<0.05) =	Ageing: 0.329	Genotype: 0.38	A×G: 0.658
SEM± =	Ageing: 0.153	Genotype: 0.177	A×G: 0.306	SEM± =	Ageing: 0.112	Genotype: 0.129	A×G: 0.224

Letters in superscript indicate significant differences at p<0.05 using the LSD tests; Values in parenthesis are percent change in values with ageing over fresh seeds (0 month); A×G, Ageing × Genotype.

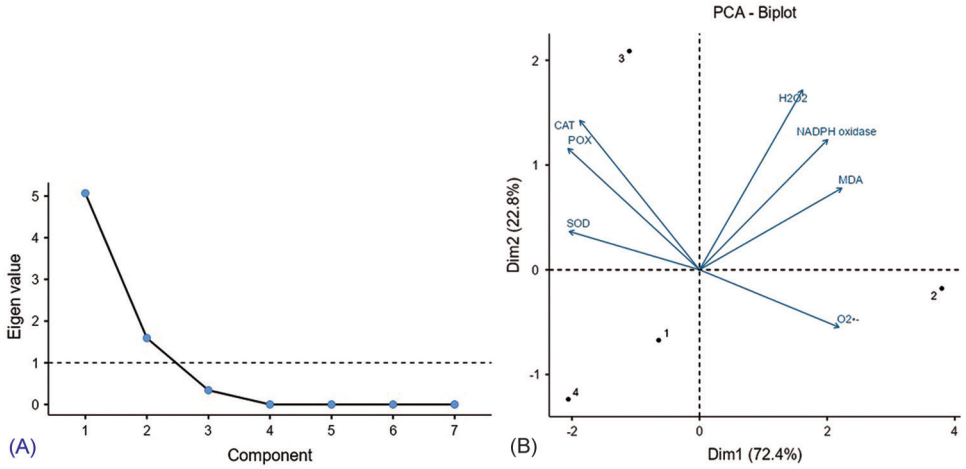

Fig. 3 (A) Scree plot indicating the Eigenvalues of components (B) PCA biplot presenting the distribution of biochemical traits in onion seeds based on their component loadings for NADPH oxidase, $O_2^{\bullet-}$, H_2O_2, MDA, SOD, CAT and POX.

reported having higher NADPH oxidase, ROS content and higher lipid peroxidation after ageing, which is responsible for seed deterioration during ageing. The decreased antioxidant enzyme activities and increased NADPH oxidase consequently resulted in accumulation of the ROS and higher lipid peroxidation, thereby resulting in higher seed deterioration in POS 24K and Bhima Shubhra leading to their poor storability, as compared to Sukhsagar and Bhima Super irrespective of the initial germination percentage. The higher NADPH oxidase activity and higher accumulation of ROS during initial 6 months of storage as compared to later 6 months of storage can be related to decreased antioxidant enzyme activity with a decline in germination with respective ageing. The decline in seed germination percentage was found to be positively correlated with SOD, CAT and POX activity, and negatively correlated with NADPH oxidase, superoxide, H_2O_2 and MDA content indicating their role in seed deterioration. The study strengthens our understanding of the impact of initial seed quality on antioxidant enzymes in amending the negative role of ROS and indicated a direct relation with the seed germination efficiency of aged onion seeds.

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