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RESEARCH ARTICLE

Impact of projected climate on seed longevity in rice

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Abstract

The resultant seed quality of harvested seeds from elevated CO_2 conditions over a prolonged storage period has not been widely investigated. Seed deterioration during storage poses a critical challenge to agricultural sustainability. This process involves various physical, physiological and biochemical changes in seeds, which can lead to reduced viability and germination rates. These changes are often caused by inadequate or improper storage conditions, which fail to provide the necessary systematic approaches to preserve seed quality over time. The study evaluated the impact of different storage conditions on rice cultivar CO 51 seeds grown in elevated CO_2 conditions. Rice seeds were packed in various packaging materials, *viz*., gunny bag, polythene bag and plastic container, stored in ambient storage (27° ± 2 °C/ CO_2 400 ppm) and elevated CO_2 (550 ppm). The results indicated that prolonged storage under ambient conditions leads to a decline in physiological seed quality, membrane damage, impaired biosynthetic reactions and a weakened antioxidant defence system, all contributing to seed deterioration. In contrast, seeds stored in elevated CO_2 conditions showed the best preservation of seed viability and biochemical properties with minimal deterioration. These findings suggest elevated CO_2 conditions are ideal for maintaining seed longevity, ensuring seed quality is preserved until the next planting season.

Keywords: deterioration; elevated CO_2; rice; storage environment; seed viability

Introduction

Success in agriculture depends on the ability of seeds to stay viable till the next sowing season under atmospheric storage conditions, for which high physiological seed quality is essential. Seed deterioration involves physical, physiological and biochemical changes in seeds, further reducing the viability and ultimately causing the seeds' death (1). This is due to the inadequacy of seed storage methods, which scientific storage methods can overcome. The storage of seeds is influenced by both biotic and abiotic factors (2). In addition to biotic agents like insects, fungi and rodents and the consequences of improper handling during sampling and testing, biotic elements that impact seeds include their genetic makeup, initial quality, provenance and moisture content. On the other hand, abiotic factors include ambient aspects such as temperature, relative humidity, gaseous atmosphere, storage cleanliness and the properties of packaging materials (3).

Seed vigour is affected by several environmental factors during storage (4). Atmospheric O_2 is considered an essential factor in regulating seed longevity during storage. The primary damage during storage is due to increased respiration, leading to seed deterioration. The increase in O_2 will increase the respiration rate, thereby increasing the deterioration rate at high temperatures and low relative humidity (RH) (5). There are also reports suggesting that due to increased O_2, the increase in free radical production and accumulation will also have adverse effects on seeds by depleting the antioxidant defence mechanisms. High RH and temperature rapidly hasten seed deterioration and thereby reduce the physiological ability of the seeds to survive. Seeds are subjected to high temperatures and moisture, which helps control decline (6).

α-amylase enzyme activity is essential in starch metabolism and provides metabolic force during seed germination. Reducing its activity during storage will drastically affect the seed quality (7). Catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD) are examples of antioxidant enzymes that are essential for protecting seeds against oxidative stress. When this antioxidant defence system is less effective during storage, reactive oxygen species (ROS) can build up and cause cellular damage, viability loss and cell death (8). So, as a result of all these factors, seed leachates' electrical conductivity will increase due to the weakening of the cell organelle membrane and the decrease of membrane phospholipids, indicating a higher rate of respiration and increased metabolic activity.

Modified atmosphere (MA) with elevated CO_2 is one of the techniques used to maintain seed viability and preserve the seeds from deterioration. The MA storage is achieved by replacing oxygen with CO_2, thereby reducing the respiration rate of seed deterioration. So, it can be an effective method against seed deterioration and reduce the activity of insects and microorganisms in the seed (9). A high CO_2/O_2 ratio is possibly advantageous for maintaining seed longevity during prolonged seed storage (10). The studies aimed to find the effect of regular seeds under modified conditions. However, changing climatic conditions, such as increased CO_2 in the atmosphere, will impact seed quality and longevity under different storage conditions. This study assessed how seeds harvested in an open-top chamber with elevated CO_2 levels (550 ppm) were affected physically, physiologically and biochemically by the storage of a modified atmosphere (MA).

Materials and Methods

Experimental design

The field experiment was carried out during 2020 and 2021 at the Wetland Farm, Department of Farm Management, Tamil Nadu Agricultural University, Coimbatore, using the rice variety CO 51, which was cultivated in an open-top chamber (OTC) with enhanced CO_2 circumstances (550 ppm). Situated at latitude 11°N and longitude 77°E, the location is 427 m above mean sea level (11).

The laboratory tests were conducted at the Department of Seed Science and Technology, Tamil Nadu Agricultural University, Coimbatore, using seeds collected from the field study between June 2021 and July 2022. A complete randomized block design, including four replications, was used to analyze the data.

Rice seeds were dried until they reached a safe moisture content of 13 per cent. Seed samples were packed in different containers, such as gunny bags (GB), polythene bags (PB) and plastic containers (PC). After filling, seeds were stored under two environmental conditions: 1) atmospheric storage (AS) and 2) elevated CO_2 (eCO_2) conditions. In AS, the seeds are stored in a gunny and polythene bag at the normal room temperature of 27 ± 2 °C, 70±5 % RH and 400 ± 9 ppm CO_2. For eCO_2 conditions, the seeds were packed in a plastic container with eCO_2 (550 ppm) and kept at room temperature for 12 months. CO_2 was filled into the plastic container by the flushing method. The container was airtight with petroleum jelly and had a rubber septum, an inlet port and an outflow port on the lid. The outlet port was used to release the displaced gas and the intake port was used to inject carbon dioxide (CO_2) gas. To reach 550 ppm concentration, CO_2 was discharged into the plastic container and measured using a CO_2 analyzer (Model: Dansensor).

Physiological and biochemical parameters

The hot air oven method measured the moisture content every two months. The International Seed Testing Associations' (ISTA) requirements were followed in evaluating rice seeds' dry matter production, seedling length and germination percentage (12). Seed germination per cent was calculated as per the Equation 1 formulae.

$$\text{Germination per cent} = \frac{\text{Seeds germinated}}{\text{Total seeds}} \times 100 \qquad \text{(Eqn. 1)}$$

Vigour index was computed by the formula in Equation 2 (13)

$$\text{Vigour index} = \text{Germination per cent} \times \text{Total seedling length (cm)} \qquad \text{(Eqn. 2)}$$

The determination of α amylase activity (mg maltose min^{-1}), starch content (mg g^{-1}), protein content (%) and dehydrogenase activity (OD g^{-1} seeds) was according to the standard protocols (14, 15, 16, 17). Also, the Electrical conductivity (dS m^{-1}), free sugar (µg mL^{-1}) and free amino acid (µg mL^{-1}) content were measured using the standard methods (18-20), respectively. The antioxidant enzyme such as catalase activity (µmol H_2O_2 $min^{-1} g^{-1}$ protein), peroxidase activity (µ mg^{-1}protein min^{-1}) and superoxide dismutase (µ mg^{-1}protein min^{-1}) activity was determined (21, 22, 23).

Statistical analysis

The data are based on three independent measurements and are shown as mean ± standard error. Using one-way ANOVA, statistical analysis was conducted using SPSS software version 24.0 (SPSS Inc., Chicago, IL, USA). $P < 0.05$ was the significance level for Duncans' Multiple Range Test (DMRT), which was used to identify significant differences between treatments.

Results

The impact of elevated CO_2 due to climate change on rice seed storage was studied using modified conditions from 2021 to 2022. The variations of different quality parameters *viz*, physical, physiological, biochemical and antioxidant enzyme activity of the seeds are presented in this chapter. The changes in seed moisture content (MC) in GB, PB and PC under AS and eCO_2 conditions are presented in Table 1. The MC of rice seeds

Table 1. Effect of different storage conditions on moisture content of rice seeds

Storage conditions	P_0	P_2	P_4	P_6	P_8	P_{10}	P_{12}
Gunny bag	12.4 ± 0.19^{a}	12.5 ± 0.22^{a}	12.8 ± 0.25^{abc}	13.1 ± 0.14^{cd}	13.5 ± 0.18^{de}	13.9 ± 0.41^{d}	14.4 ± 0.16^{d}
Polythene bag	12.4 ± 0.19^{a}	12.4 ± 0.17^{a}	12.4 ± 0.19^{a}	12.5 ± 0.21^{ab}	12.7 ± 0.14^{abc}	12.7 ± 0.15^{abc}	13.0 ± 0.10^{bc}
Elevated CO_2 (550 ppm)	12.4 ± 0.19^{a}	12.4 ± 0.20^{a}	12.4 ± 0.17^{a}	12.4 ± 0.19^{a}	12.5 ± 0.19^{ab}	12.6 ± 0.11^{ab}	12.7 ± 0.16^{abc}
Mean	12.4	12.4	12.5	12.7	12.9	13.1	13.4

exhibited an increasing trend concerning the prolonged storage period under the AS condition compared to the eCO_2 condition. Gunny bag storage exhibited the highest increase in MC (14.4) followed by PB (13.0), while minimum MC was recorded in PC (12.7) under the eCO_2 condition.

Physiological seed quality parameters

The vigour index (VI), dry matter production (DMP), root length (RL), shoot length (SL), germination percentage (G %) and other physiological seed quality metrics were assessed for rice seeds kept in different storage settings and for various amounts of time (Tables 2-6). As the duration of storage increased, all physiological characteristics of seeds kept under ambient storage (AS) conditions significantly declined. Among the containers under AS condition, decreases in G %, RL, SL, DMP and VI were minimal in a polythene bag. A significant decrease in physiological seed quality characters was observed in a gunny bag. However, the quality parameters of seeds stored under eCO_2 did not decline with a prolonged storage period. At the end of the storage period, maximum G %, seedling length, DMP and VI were observed in the eCO_2 condition.

Biochemical seed quality parameters

A pictorial illustration of biochemical seed quality parameters and antioxidant enzyme activity of rice seeds stored in different containers under different environmental conditions are presented in Fig. 1a-1d and Fig. 2a-2c). The α-amylase activity, starch, protein and dehydrogenase activity in rice seeds was reduced significantly under different storage conditions. The reduction rate varied according to the storage conditions and the maximum was observed in the GB under AS. The α-amylase activity drastically reduced GB in AS (42 %), while the reduction was minimal in eCO_2 storage. For starch and protein content, a decrease of 11.3 % and 24.6 % were observed in GB, while the reduction was only 1.1 % and 1.3 % in the eCO_2 condition. The dehydrogenase activity was reduced by 11.1 %, 2.1 % and 0.4 % in GB, PB and eCO_2 conditions, respectively. The antioxidant enzyme activity (catalase, peroxidase and superoxide dismutase) in storage showed a similar trend to other biochemical parameters during the storage. There was a minimum reduction in the eCO_2 storage conditions compared to AS in both GB and PB. At the end of the storage period, the activity reduction in eCO_2 conditions was only about 14-20 %, while in GB under AS, the reduction was about 45-60 %. The electrical conductivity (EC), free sugar and free amino acid of seed leachates differed significantly due to seed packaging and storage period (Fig. 3a-3c). At 12 months of storage, the PC-packed seeds showed the lowest EC 0.24 dS m^{-1}, free sugar 12.12 µg mL^{-1} and free amino acid (1.89 µg mL^{-1}) under eCO_2 condition. There was a

Table 2. Effect of different storage conditions on seed germination per cent of rice seeds

Storage conditions	P_0	P_2	P_4	P_6	P_8	P_{10}	P_{12}
Gunny bag	95±0.41^a	94±0.95^{ab}	92±1.11^{bc}	90±1.35^{cd}	88±0.41^d	84±0.41^d	79±0.95^c
Polythene bag	95±0.41^a	95±0.95^a	95±0.71^a	93±1.35^{ab}	90±0.25^{cd}	88±0.75^c	86±0.71^{bb}
Elevated CO_2 (550 ppm)	95±0.41^a	95±1.11^a	95±0.71^a	95±0.95^a	94±0.95^{ab}	94±1.35^{ab}	92±0.41^{ab}
Mean	95	95	94	93	91	89	86

Data presented are means from four replicates with standard errors. Within each treatment, different letters at each column indicate significant differences by Duncans' multiple range test at P<0.05.P – Storage period

Table 3. Effect of different storage conditions on shoot length (cm) of rice seeds

Storage conditions	P_0	P_2	P_4	P_6	P_8	P_{10}	P_{12}
Gunny bag	8.3±0.11^a	8.2±0.09^{ab}	8.0±0.04^c	7.8±0.11^d	7.4±0.08^c	7.0±10^c	6.5±0.09^{cd}
Polythene bag	8.3±0.11^a	8.3±0.10^a	8.2±0.07^{ab}	8.1±0.11^{bc}	7.9±0.04^{bd}	7.6±0.09^{bd}	7.2±0.10^{bd}
Elevated CO_2 (550 ppm)	8.3±0.11^a	8.3±0.07^a	8.2±0.09^a	8.2±0.04^{ab}	8.0±0.06^{ad}	7.9±0.15^{ad}	7.8±0.12^a
Mean	8.3	8.3	8.1	8.0	7.8	7.5	7.2

Table 4. Effect of different storage conditions on root length (cm) of rice seeds

Storage conditions	P_0	P_2	P_4	P_6	P_8	P_{10}	P_{12}
Gunny bag	15.4±0.24^a	15.2±0.20^{abcd}	15.0±0.11^{bcd}	14.5±0.24^{ef}	14.0±0.07^g	13.4±0.14^g	12.5±0.17^{ce}
Polythene bag	15.4±0.24^{ab}	15.3±0.18^{ab}	15.2±0.09^{abc}	15.0±0.03^{abcd}	14.8±0.17^{cde}	14.5±0.20^{ef}	14.1±0.07^{bd}
Elevated CO_2 (550 ppm)	15.4±0.24^{ab}	15.3±0.06^{ab}	15.3±0.14^{ab}	15.2±0.24^{abcd}	15.0±0.16^{abcd}	15.0±0.05^{abcd}	14.8±0.10^{ad}
Mean	15.4	15.3	15.2	14.9	14.6	14.3	13.8

Data presented are means from four replicates with standard errors. Within each treatment, different letters at each column indicate significant differences by Duncans' multiple range test at P<0.05. P – Storage period

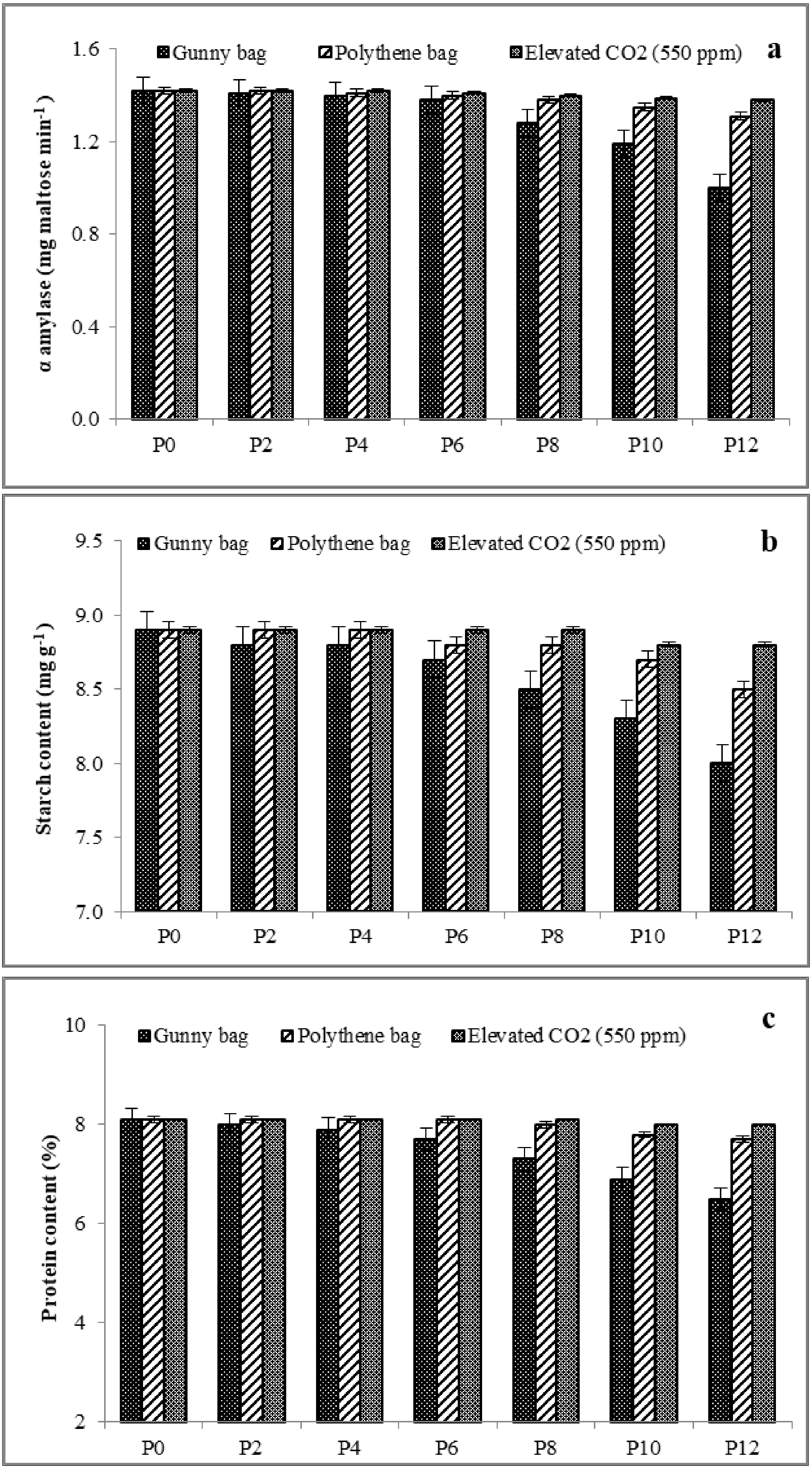
Table 5. Effect of different storage conditions on dry matter production (mg 10 $seedlings^{-1}$) of rice seeds

Storage conditions	P_0	P_2	P_4	P_6	P_8	P_{10}	P_{12}
Gunny bag	98±1.4^a	96±1.7^{ab}	92±1.3^{cde}	89±0.9^{de}	83±1.1^e	78±1.4^c	61±1.1^c
Polythene bag	98±1.4^a	97±1.3^{ab}	97±0.7^{ab}	95±1.0^{abc}	92±0.8^{cd}	89±1.1^b	85±0.9^{bb}
Elevated CO_2 (550 ppm)	98±1.4^a	98±1.5^a	98±1.1^a	96±1.4^{ab}	96±1.3^{ab}	94±1.6^a	90±1.4^{ab}
Mean	98	97	96	93	90	87	79

Table 6. Effect of different storage conditions on vigour index of rice seeds

Storage conditions	P_0	P_2	P_4	P_6	P_8	P_{10}	P_{12}
Gunny bag	2254±12^a	2206±12^{abc}	2120±10^{cb}	2007±15^{ef}	1883±13^i	1714±13^j	1508±15^k
Polythene bag	2254±12^a	2248±11^a	2226±11^{ab}	2148±12^{cd}	2037±12^{bg}	1960±15^h	1872±11^i
Elevated CO_2 (550 ppm)	2254±12^a	2250±12^a	2235±12^a	2229±14^{ab}	2168±11^{abd}	2153±12^{cd}	2077±15^{ef}
Mean	2254	2235	2193	2128	2029	1942	1819

Data presented are means from four replicates with standard errors. Within each treatment, different letters at each column indicate significant differences by Duncans' multiple range test at P<0.05


a
Gunny bag
Polythene bag
Elevated CO2 (550 ppm)
α amylase (mg maltose min-1)
1.6
1.2
0.8
0.4
0.0
P0
P2
P4
P6
P8
P10
P12
b
Gunny bag
Polythene bag
Elevated CO2 (550 ppm)
Starch content (mg g-1)
9.5
9.0
8.5
8.0
7.5
7.0
P0
P2
P4
P6
P8
P10
P12
c
Gunny bag
Polythene bag
Elevated CO2 (550 ppm)
Protein content (%)
10
8
6
4
2
P0
P2
P4
P6
P8
P10
P12

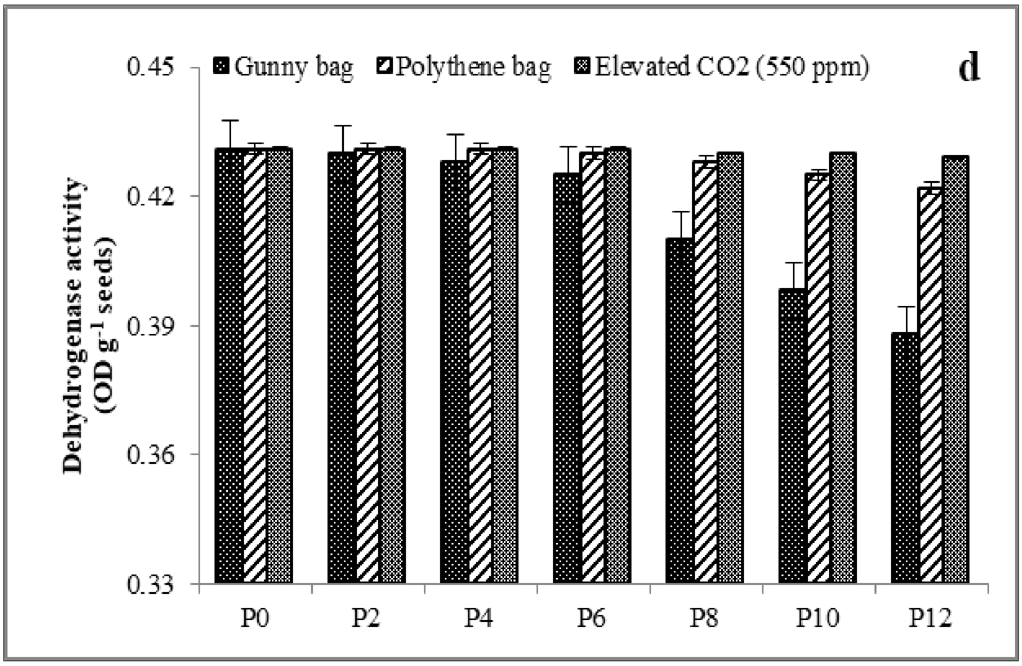
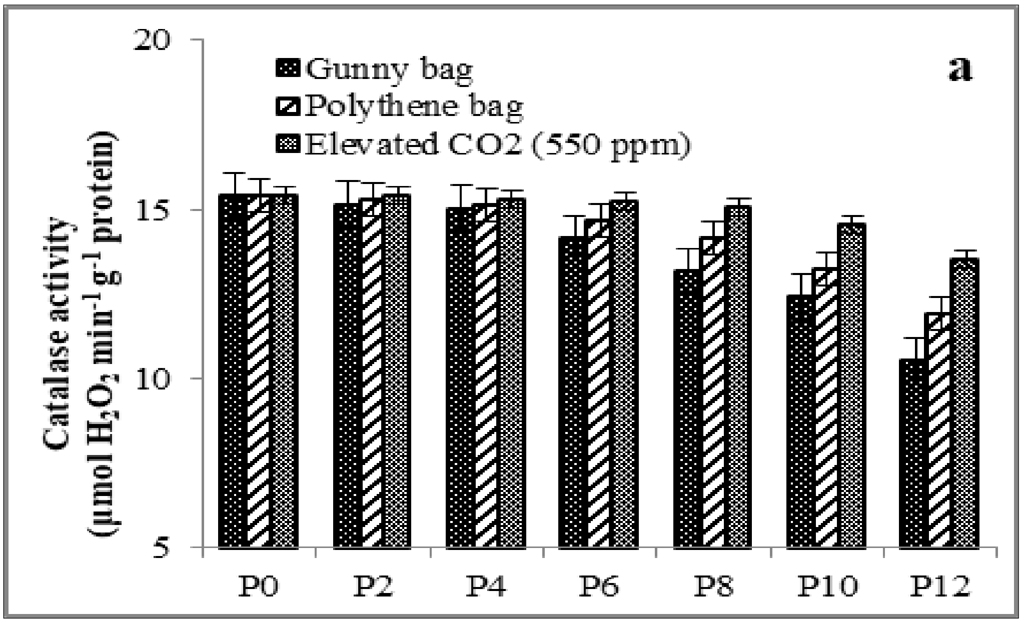
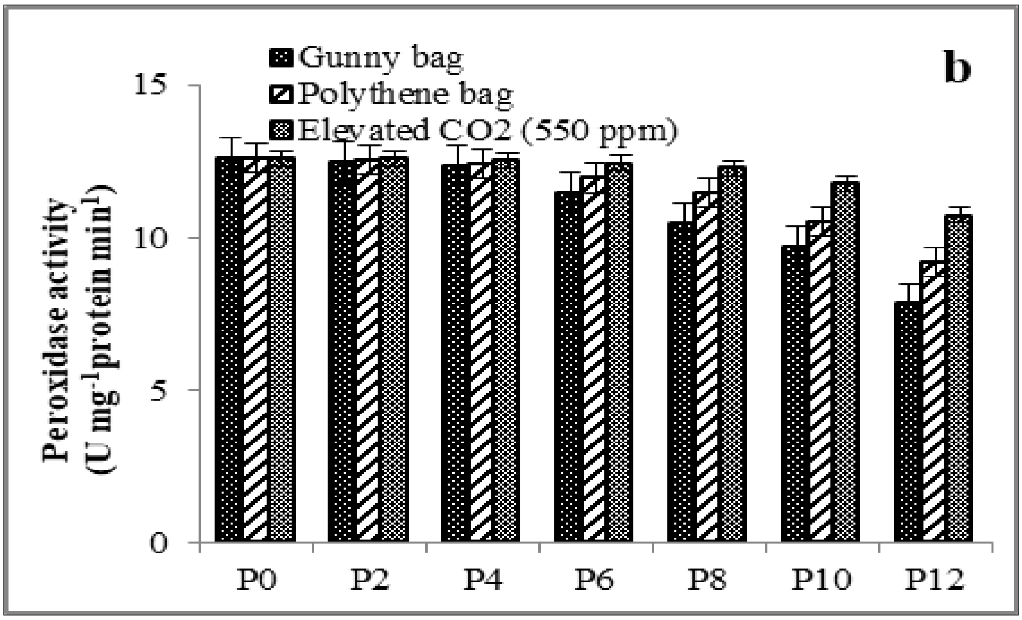


Fig. 1. Effect of different storage conditions on a) α amylase (mg maltose min^{-1}), b) Starch content (mg g^{-1}), c) Protein content (%) and Dehydrogenase activity (OD g^{-1} seeds) of rice seeds P - Storage period.





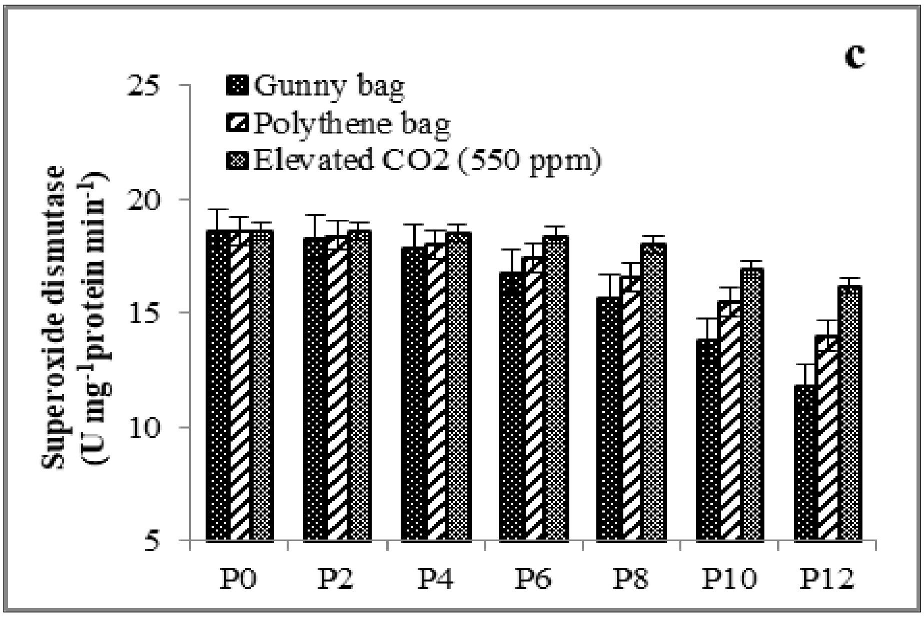
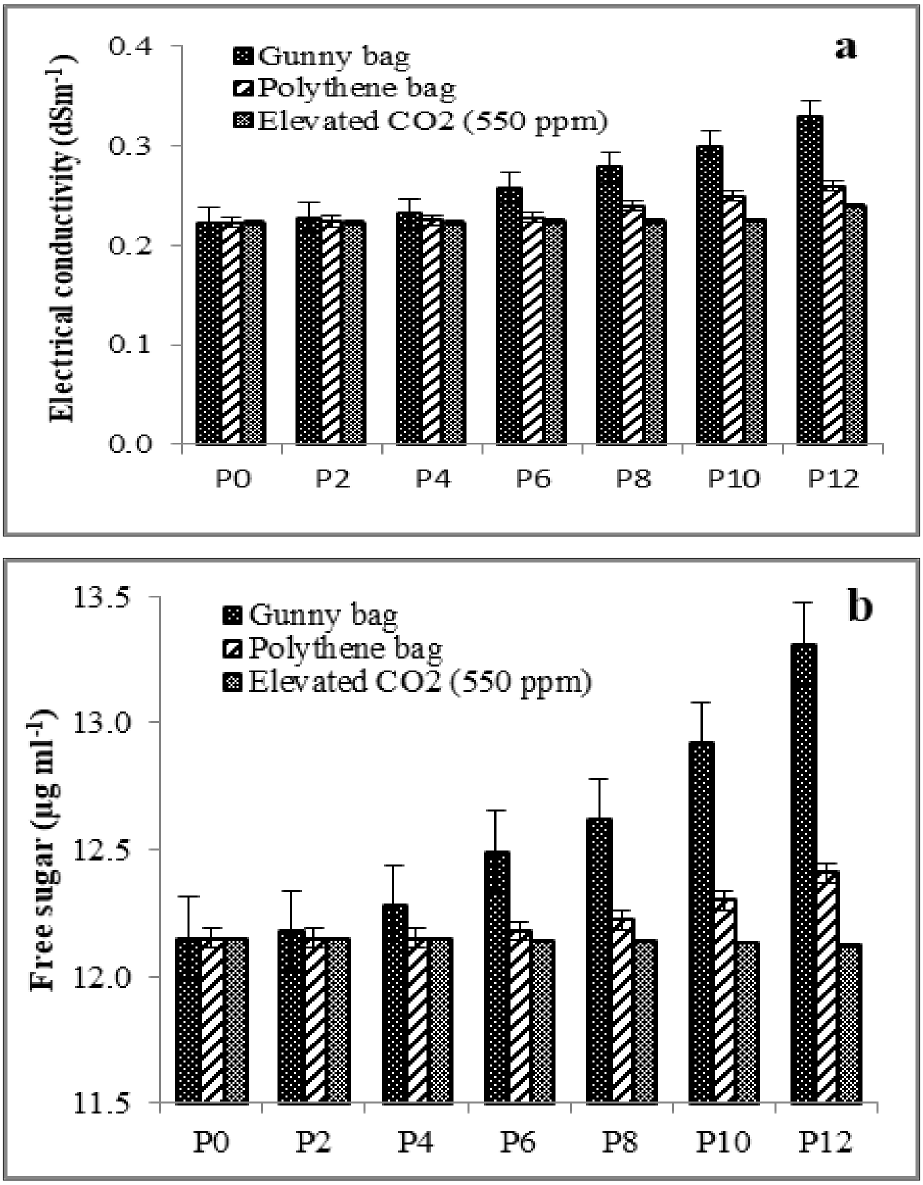


Fig. 2. Effect of different storage conditions on a) Catalase activity (µmol H2O2 min^{-1} g^{-1} protein) b) Peroxidase activity (µ mg^{-1}protein min 1) c) Superoxide dismutase (µ mg^{-1} protein min^{-1}) of rice seeds P - Storage period.



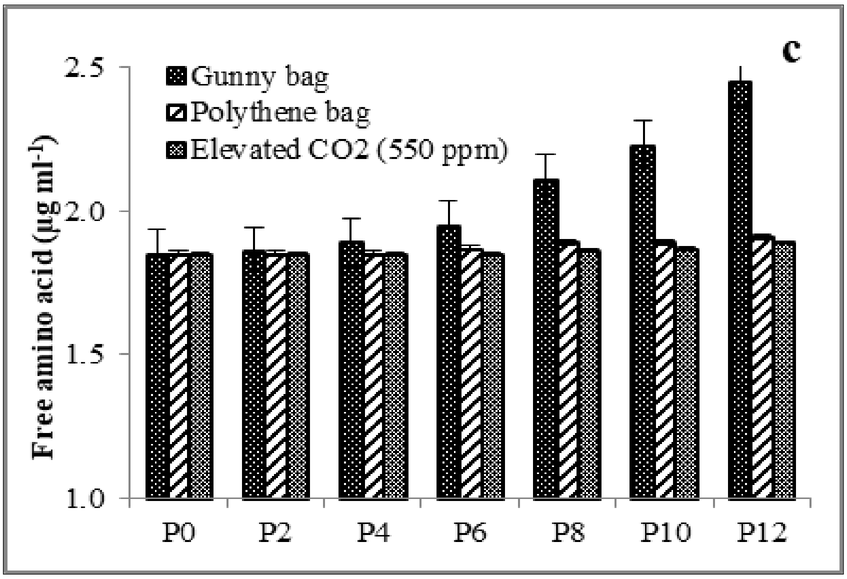


Fig. 3. Effect of different storage conditions on a) Electrical conductivity (dS m^{-1}) b) Free sugar (µg mL^{-1}) c) Free amino acid (µg mL^{-1}) of rice seed. P: Storage period.

significant increase in EC, free sugar and free amino acid from (0.22 to 0.33 and 0.26 dSm^{-1}), (12.6 to 13.31 and 12.4 µg mL^{-1}) and (1.85 to 2.45 and 1.91 µg mL^{-1}) in seeds packed in GB and PB under AS condition with prolonged period of storage (Figure 2a to 2c).

Discussion

Seeds are hygroscopic and absorb moisture from the surrounding air. The variation in RH and temperature directly impacts the increased moisture content of stored seeds. However, higher seed moisture was observed when the seeds were packed in GB followed by PB due to high permeability, allowing the seeds to contact the surrounding environmental conditions (24). The advantage of PB over GB in seed storage is that it can increase the seed longevity during storage. The same trend was observed in the efficiency of storage material in keeping the moisture content constant. The eCO_2 condition, which has the least contact with the environment, showed the minimum increase in the seed moisture content. The seed longevity decreased under ambient oxygen conditions due to a rise in respiration rate (25). The eCO_2 storage provides protection and maintains persistent moisture content during seed storage. Also, this modified atmospheric storage reduces seed respiration, which may eventually lead to seed deterioration. The seed respiration was found to be increased with high seed moisture and the presence of increased oxygen (26). In eCO_2 seed storage, the O_2 content inside the container is reduced and the CO_2 concentration rises to a level where aerobic respiration is diminished. The low O_2/ high CO_2 helps in low permeability and maintains persistent moisture content during storage. The viability of seeds was maintained under the eCO_2 condition, which is possible because when it is isolated from normal environmental conditions, the moisture content in the seed will be constant (27).

Proper seed storage is essential to ensure food supply by maintaining seed quality and vigour in adverse environmental conditions. Appropriate seed packaging and controlled storage conditions can also protect the seeds from deterioration during storage (28). The decline in seed germination per cent under ambient seed storage is due to fluctuations in temperature, RH and moisture content (2). Losses of seed germination potential and vigour index due to depletion of food reserves under ambient conditions result in several changes caused by respiration (29). The present study found that the seed germination and seedling vigour of stored seeds were significantly reduced when the seeds were packed in GB followed by PB under ambient conditions due to the influence of O_2, RH and temperature, which are known factors influencing the seed viability during storage. In contrast, no significant decrease was found in seeds stored under the eCO_2 condition.

Starch mobilization is an essential metabolic process that stimulates seed germination (30). This study found that variations in temperature, meteorological conditions and relative humidity (RH) caused a notable drop in the nutritional content of seeds during storage. However, because of the limited environmental influence, the nutrient decrease was negligible under increased CO_2 (eCO_2) circumstances. Similar patterns under various storage settings have been documented in earlier research. Decreased α-amylase activity, decreased total soluble sugar content and depletion of endosperm food reserves are the causes of the reduction in starch metabolism during extended storage, which eventually affects seed viability and germination efficiency. α-Amylase plays a crucial role in seed germination by breaking stored starches into sugars, providing the necessary energy for the growing seedling. During storage, the activity of α-amylase can decrease due to factors like oxidative stress, ageing, or improper storage conditions. This reduction in enzyme activity limits the seeds' ability to mobilize starch reserves efficiently, which can lead to delayed or incomplete germination. Seeds with reduced α-amylase activity may exhibit slower or weaker seedling development, resulting in lower emergence rates and potentially stunted growth (31).

Elevated antioxidant enzyme activity (CAT, POD, SOD) under elevated CO_2 conditions plays a vital role in enhancing seed longevity by mitigating oxidative stress, reducing lipid peroxidation and preventing membrane damage. These enzymes serve as reliable markers of seed quality, correlating with improved viability and vigour. Customizing storage environments, such as maintaining elevated CO_2 levels, preserves enzymatic defences, delaying seed deterioration and minimizing dependency on chemical preservatives. This eco-friendly approach ensures sustainable storage practices. While focused on rice, these findings have broad applicability across crops, highlighting the potential for elevated CO_2 systems to enhance seed storage and maintain quality long-term. The reduction in the antioxidant enzymes was significant in the AS conditions and minimal in the controlled conditions. This might be due to external conditions like high RH and ambient oxygen, which increase seed moisture content, thereby increasing the respiration and loss of seed reserves (32). The change in metabolic activities would trigger the accumulation of free radicals, which eventually reduces the protein, membrane disintegration and inactivation of antioxidant enzymes (33).

The accumulation of free radicals causes a reduction in starch metabolism in seeds and impairs the anti-oxidative system. The increase in EC in seed leachate observed in AS may be due to the loss of membrane integrity (33). The increase in free sugar and amino acid content is observed in AS. This shows that the exhaustion of organic compounds, which is detrimental to seed longevity and membrane loss due to increased stored seeds, leads to seed deterioration (34).

Elevated CO_2 storage conditions enhance seed longevity by creating an environment that reduces oxidative stress, a significant factor in seed deterioration during storage. Under traditional storage conditions, seeds are exposed to ambient oxygen levels, facilitating the production of reactive oxygen species (ROS). These ROS cause lipid peroxidation, membrane damage and degradation of essential biomolecules, leading to a decline in seed viability over time. Elevated CO_2 conditions suppress oxidative damage by lowering oxygen availability and enhancing the activity of antioxidant enzymes such as catalase (CAT), peroxidase (POD) and superoxide dismutase (SOD). These enzymes neutralize ROS, maintaining seed vigour and biochemical stability.

This improvement in seed storage directly addresses broader agricultural challenges, such as food security and the need for sustainable farming practices. Prolonged seed viability ensures a reliable supply of high-quality seeds, reducing the need for frequent seed regeneration and minimizing waste. Moreover, it supports farmers in regions with limited access to fresh seeds, enabling long-term storage for future planting seasons. By reducing dependency on chemical preservatives, elevated CO_2 storage also aligns with global efforts to adopt environmentally friendly agricultural practices, addressing the dual goals of sustainability and productivity.

Conclusion

The study concludes that rice seeds of cultivar CO 51 grown under elevated CO_2 conditions exhibit better preservation of seed quality during storage compared to ambient storage conditions. Seeds stored in elevated CO_2 (550 ppm) maintained higher viability and biochemical stability with reduced physiological deterioration, membrane damage and oxidative stress. Packaging also influenced storage outcomes, with plastic containers providing better protection. These findings highlight the potential of elevated CO_2 environments to enhance seed longevity by mitigating deterioration, making them a promising approach for maintaining seed quality over prolonged storage periods, ensuring viability until the next planting season.

Future studies could explore the long-term impacts of elevated CO_2 storage conditions on a broader range of rice cultivars to confirm the generalizability of these findings. Additionally, investigating the molecular mechanisms underlying enhanced seed quality and reduced oxidative stress under elevated CO_2 could provide deeper insights. The interaction between elevated CO_2 levels and other environmental factors, such as temperature and humidity, during storage warrants further examination. Studies could also evaluate the economic feasibility and scalability of implementing elevated CO_2 storage systems in large-scale seed storage facilities. Finally, examining the effects of elevated CO_2 storage on other crop species could expand its application for global agricultural sustainability.

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Authors' contributions

VM designed the study. VN experimented and drafted the manuscript. SM, KS, TA and JD assisted in analysing and drafting the manuscript's final version and MP and PT did the statistical analysis. All authors read and approved the final manuscript

Compliance with ethical standards

Conflict of interest: Authors do not have any conflict of interest to declare.

Ethical issues: None

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