



RESEARCH COMMUNICATION

# Understanding seed longevity in rice under variable temperature conditions

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Received: 20 September 2025; Accepted: 21 April 2026; Available online: Version 1.0: 27 August 2026

**Cite this article:** Swastideepa S, Sharat KP, Jyotirmayee M, Nabaneeta B, Gaurav K, Simanta M, Devraj L, Manasi D, Swapan KT, Subhendu SS, Priyadarsini S. Understanding seed longevity in rice under variable temperature conditions. *Plant Science Today*. 2026;13(sp5):01–10. <https://doi.org/10.14719/pst.11875>

## Abstract

A study involving fifty rice germplasm lines was conducted to investigate the effect of variable temperature and relative humidity ( $30 \pm 2^\circ\text{C}$  for 90 days, followed by  $50 \pm 2^\circ\text{C}$  for two days at 60–70 % relative humidity (RH)) on seed longevity traits. The results confirmed a sharp decline in germination percentage (GP), speed of germination (SOG), seedling length (SL) and seed vigour index-I (SV-I) when compared to the quality of freshly harvested ones. The comparative analysis showed a significant positive correlation between GP and SOG (0.95) and between GP and SV-I (0.87). The fifty genotypes were grouped into three clusters, based on the similarities of behaviour under the treatment. The principal component analysis (PCA) also confirmed the grouping of the genotypes based on the seed quality traits under variable temperature treatments. The traits such as GP and SV-I were found highly affected on storage of seed at ambient temperature ( $30 \pm 2^\circ\text{C}$ ) followed by a sudden increase in temperature ( $50 \pm 2^\circ\text{C}$ ). Genotypes such as MDU-5, Manavari, Radhabati and PMK2 have showed least decrease in seed quality traits under variable temperature treatment. These germplasm lines could be used as suitable donor for development of climate resilient varieties which can ensure high-quality seed storage policies in future.

**Keywords:** germination percentage; high temperature; longevity; rice; seed; seed quality

## Introduction

Seed quality is the fundamental basis of agricultural production, which directly affects the successful establishment of crops, yield potential and food security. Among the various characteristics in determining the seed quality, viability and vigour are the most important. Viability means the ability of seeds to germinate under suitable conditions (1). On the other hand, vigour is the ability of seeds to germinate rapidly and develop into healthy seedlings. The seed quality and viability during storage depend upon the initial quality of seed and the way it is stored (2). As an inevitable process, seed ageing leads to a gradual decline in longevity over time (3). Rice (*Oryza sativa* L.), a staple food crop for a large proportion of the world's population, requires maintenance of seed quality during storage to ensure sustainable production. Seeds are hygroscopic in nature, which increases the potential for moisture-induced degradation. Rice being an orthodox seed can be desiccated to minimum moisture content of 13 % and could be stored for sowing

in the next season (4). Storage conditions, whether normal or moisture-impervious, depend largely on seed moisture content. However, in large-scale storage systems, not only seed moisture but also external environmental factors play a vital role in determining seed longevity and quality. A complex interaction of genetic and environmental factors influences seed viability and quality during storage (5). The major factors affecting seed longevity include temperature, relative humidity, seed moisture content and oxygen availability. High temperature and relative humidity accelerate seed deterioration, resulting in loss of viability and vigour (6).

During storage, seed deterioration is characterised by a range of biological and biochemical changes (7). In Cuttack, Odisha seeds stored after harvest (during the month of December) are exposed to a temperature of  $28\text{--}30^\circ\text{C}$  (January–March) during storage. Thereafter seeds are subjected to sudden rise in temperature of  $40\text{--}45^\circ\text{C}$  during the month of April–May. High temperatures destroy the integrity of the seed membrane, leading to protein denaturation and

disruption of essential enzymatic functions (8). Furthermore, oxidative stress increases during storage due to the accumulation of reactive oxygen species (ROS), which have deleterious effects on cellular components such as lipids, proteins and nucleic acids (9–10). These changes result in reduced germination rate, delayed seedling development and impaired vigour. Climate change poses a profound challenge to seed storage, especially with increasing temperatures and extreme moisture trends. As this change progresses, it becomes increasingly difficult to maintain seed quality. In regions like South Asia, where rice is the main food crop, the impact of this change is particularly severe. Some alternative methods have been proposed to prevent seed loss from high-temperature storage. The most important of these is controlled environment-based storage where temperature and humidity are controlled (11). While temperature and humidity have been identified as key factors in seed storage, it is not clear how effective treatment-based methods are effective under such constant temperature stress. Thus, understanding the effect and severity of the storage condition is essential for storage of seeds.

The aim of this study is to simulate the environmental condition in order to investigate the effect of temperature variation on fifty rice germplasms. For this, the control was compared to a treatment which was stored at room temperature ( $30 \pm 2^\circ\text{C}$ ) and relative humidity (RH), followed by  $50 \pm 2^\circ\text{C}$  for 2 days under 60–70 % RH. The response of seeds to heat stress was measured through parameters like germination percentage, speed of germination, seedling length and seed vigour index-I at constant initial seed moisture content. The results of this study will provide insights into the biological mechanisms of seed under high temperatures and form the basis for future high-quality seed storage policies. Understanding how temperature variation affects seed quality, which will be helpful in developing appropriate storage systems and safeguarding agriculture in the face of climate change by development of climate resilient varieties.

## Materials and Methods

### Selection of experimental material

A set of fifty diverse rice germplasm from various regions of India were collected from Gene Bank, Indian Council of Agricultural Research-Central Rice Research Institute (ICAR-CRRI), Cuttack for the study of seed longevity under variable temperature conditions. The seeds were multiplied in the field of ICAR-CRRI, Cuttack during kharif 2021–2022 following randomised block design. After harvest, the moisture of the seed lot was reduced to safe moisture content of 13 %. The seeds were then treated to break dormancy ( $45 \pm 2^\circ\text{C}$  constant temperature for 3 days) (12) and seed quality traits like germination and seed vigour were recorded after the harvest of seed.

### Treatment for variable temperature in laboratory

The fifty rice genotypes were packed in separate cloth bags and stored at room temperature at  $30 \pm 2^\circ\text{C}$  for 90 days followed by exposing to high temperature at  $50 \pm 2^\circ\text{C}$  in an incubator for two days at constant RH of 60–70 %. After the completion of treatment, fifty seeds from each genotype were put for germination in three replications using top of paper method by placing moist blotting paper on it and incubating at  $30 \pm 2^\circ\text{C}$  and 60–70 % RH (13) at normal atmospheric temperature and RH i.e.  $30 \pm 2^\circ\text{C}$  at 60–70 % RH for 10 days.

### Observations for seed quality traits

Seed germination was recorded by counting number of seed germinated out of fifty seeds in each replication and the mean value was expressed as percentage in whole number. Speed of germination was calculated by the following formula given by previous researchers (14). Seedling length (cm) was measured as length from the shoot to the root tips of five seedlings for each replication and the mean value was recorded in centimetres (15). Seed vigour index (SVI) was calculated as per proposed formula for calculating seedling vigour indices (15). Freshly harvested seeds without the treatment were treated as control.

### Statistical analysis

The various data for seed longevity under control and treatment were recorded and analysed by the method of analysis of variance (ANOVA) to know the experiment's significance (16). The statistical analysis was performed using the software Python.

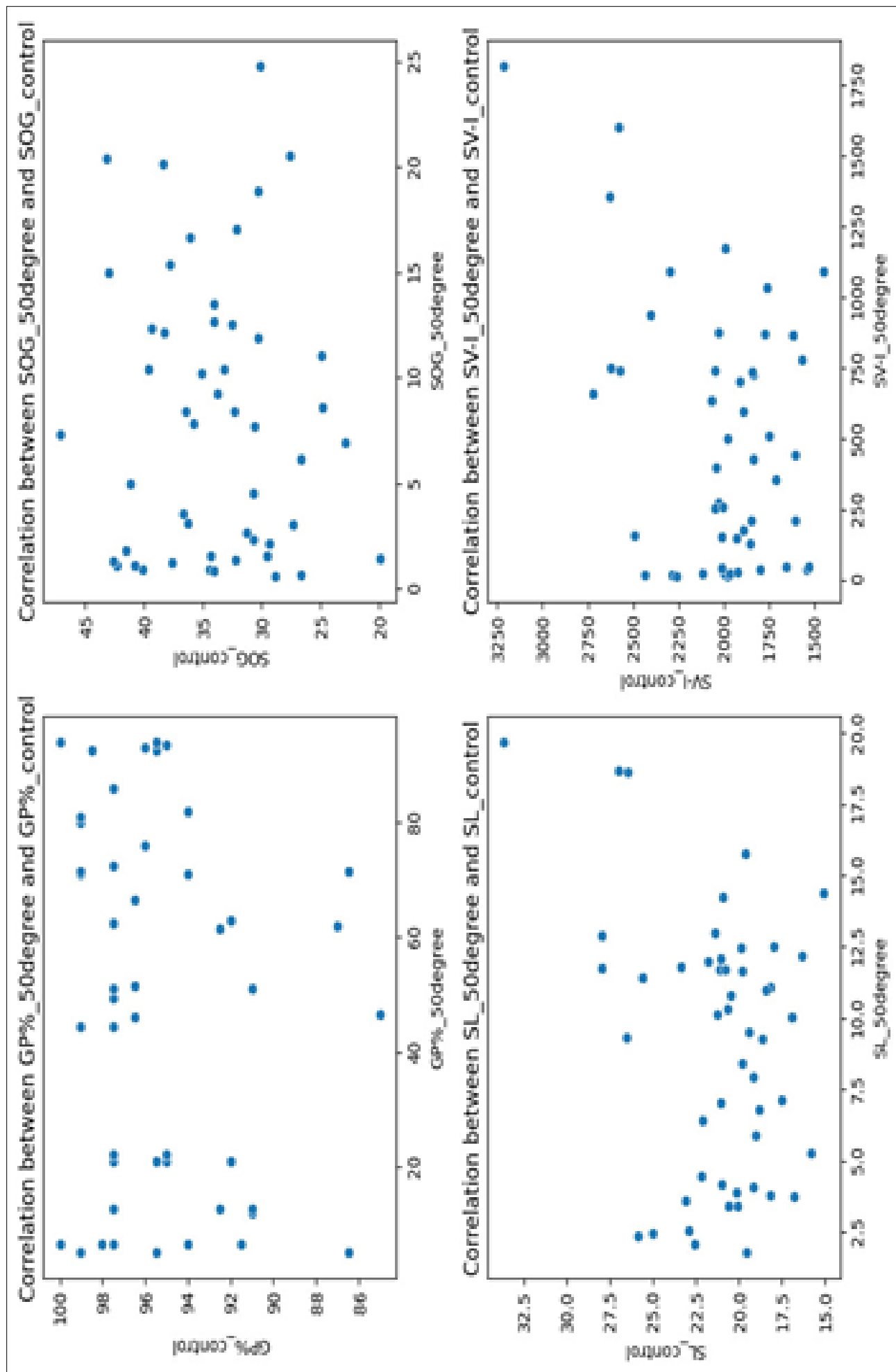
## Results and Discussion

### A comparative analysis

The comparative scatter plot analysis (Fig. 1) illustrates the relationship between seed quality traits under both control conditions and after exposure to high-temperature storage. This provides an insight into the extent of deterioration induced by thermal stress across the fifty rice genotypes. The comparative scatter plot analysis between control and treatment clearly demonstrates the detrimental effect of high-temperature storage on seed quality traits in rice.

The germination percentage (GP) showed a widespread distribution with poor correlation, indicating that most genotypes experienced a substantial decline in viability under thermal stress. The loss of consistency between GP in control and treated conditions highlights that seed viability is highly sensitive to prolonged heat exposure. A drastic decrease of 46 % average was observed in GP % of the genotypes from the initial GP % of 95 % average. Genotypes such as Swarna, Memabalbok and Champaeisali exhibited the highest reduction (more than 80 %), indicating that unfavourable storage conditions, particularly high temperature and relative humidity, accelerate seed deterioration during storage (7). In contrast, genotypes that performed comparatively well after treatment, showing less than a 10 % reduction in germination percentage, included Adira-1, MDU-5, Manavari and PMK2.

Similarly, the speed of germination (SOG) displayed moderate correlation but with significant scatter, suggesting that while a few genotypes retained germination speed, the majority exhibited delayed or inhibited germination under stress. The MDU-5, Manavari, Radhabati and PMK2 are the genotypes those performed well after treatment for the seed quality trait of SOG. Seedling length (SL) and seed vigour index (SVI) showed a weak or negligible correlation between control and treated values, implying that seedling growth and overall vigour were severely compromised by the temperature treatment. Manavari and PMK2 are the two genotypes having least decrease in seed quality traits under the treatment. Loss of vigour precedes a decrease in germination potential (16) and induces certain changes at the cellular level, e.g., the leaching of metabolites from seeds (17, 18). The drastic reductions in SV-I, which integrates both germination and seedling growth parameters, further support the conclusion that thermal



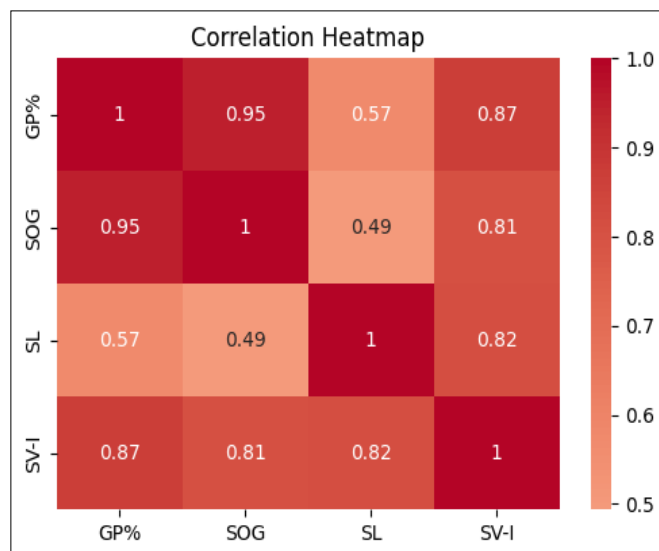
**Fig. 1.** Comparative correlation of seed quality traits under control and high-temperature storage conditions in rice genotypes.

stress significantly impairs seedling establishment potential. Germination and seedling vigour are severely affected if seed is stored at high relative humidity and deterioration is much faster if the storage temperature is also high (19).

Collectively, the data underscore the adverse effects on rice seed physiological quality and longevity due to temperature fluctuations and role of atmospheric moisture.

The distribution and box plot analysis of four key seedling performance parameters—germination percentage (GP), speed of germination (SOG), SL and seed vigour index (SVI)—under two conditions, namely prolonged ageing at room temperature for 3 months followed by 50 °C for 2 days and normal control conditions, are presented in Fig. 2. The distribution plots (Fig. 2) reveal a consistent leftward shift for the treatment group across all parameters, indicating reduced performance under heat stress. Box plots further support this observation, showing significantly lower median values for SOG, SL and SVI in the storage condition under room temperature for 3 months followed by 50 °C for 2 days, along with reduced inter-quartile ranges, suggesting a consistent negative impact of high temperature on seed germination speed, shoot growth and overall seedling vigour which is also been stated by (20). When seeds are maintained experimentally under conditions of high humidity and temperature, the rate of ageing becomes greatly accelerated and their viability falls rapidly with time (6, 20–21). Additionally, germination percentage showed increased variability under heat stress, with the presence of outliers suggesting heterogeneous responses among genotypes, consistent with findings in onion (6) and rice (20). Overall, the data clearly demonstrate the detrimental effects of sustained high temperature on seedling establishment and development.

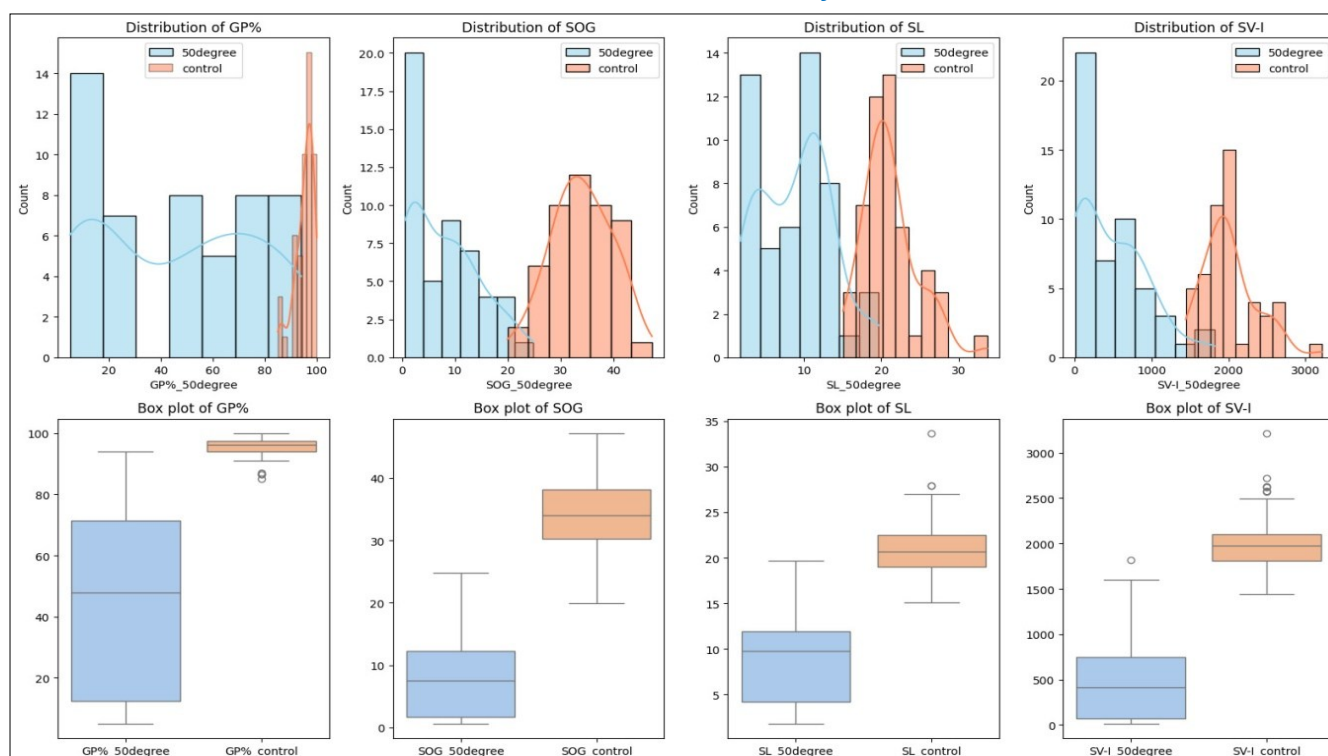
The correlation heat map (Fig. 3) illustrates the strength of linear relationships between four variables namely GP, SOG, SL and SVI under treatment. The colour intensity and numerical values represent the Pearson correlation coefficients, ranging from 0.49 to 1.0, indicating moderate to very strong positive correlations. The GP



**Fig. 3.** Heatmap for seed quality traits under variable temperature conditions in 50 rice genotypes.

shows a very strong correlation with SOG = 0.95 and SVI = 0.87, suggesting that as speed of germination or seed vigour index increase, germination percentage also tends to increase (21). This also indicates, slow germinating seeds tend to deteriorate faster. A similar trend was also seen by previous researchers (19) in sweet corn. The SL exhibits moderate correlations with GP (0.57) and SOG (0.49) but shows a strong correlation with SVI (0.82), indicating a meaningful relationship between SL and SVI (22). The strongest correlation in the matrix is between GP and SOG (0.95), highlighting the crucial role of speed of germination in determining germination percentage. The uniformly positive values indicate that none of the variables inversely affect each other, which simplifies multivariate analysis and modelling. These findings suggest the parameters are interdependent that could be a key predictive performance evaluation of seeds. Recent advances in understanding seed ageing link, vigour decline and viability loss to predict seed longevity (23).

### Cluster analysis



**Fig. 2.** The distribution and box plot analysis of four key seedling performances.

For cluster analysis, fifty rice genotypes were treated for seed longevity under varying temperature conditions. The treatment was carried out for 3 months of storage at room temperature and RH, followed by  $50 \pm 2^\circ\text{C}$  for 2 days under 60–70 % RH. The cluster analysis (Fig. 4) is selected for analysing the similarity in behaviour of various genotypes to form a group (24, 25) so that the groups of genotypes showing similar characteristics can be easily identified. Clustering provides a natural grouping of genotypes and helps distinguish them based on their characteristic trends for seed longevity. The unweighted pair group method with arithmetic mean (UPGMA)-based hierarchical clustering was used for this purpose.

From the dendrogram, three major clusters were observed, indicating distinct groupings of genotypes. The clustering pattern visually identifies natural groupings of data points, resulting in a meaningful classification of genotypes. In the generated dendrogram, there appears to be three main vertical lines that are relatively separated before merging at higher distances. The first cluster includes 26 genotypes, followed by the three genotypes in second and 21 germplasm lines in the third cluster. These clusters are further subdivided into sub-clusters at lower similarity levels based on seed quality parameters associated with longevity. This visual separation suggests that three primary clusters can broadly represent the dataset. Cluster A comprises six genotypes that are likely to exhibit moderate GP (< 70 %) and vigour (< 800) after the treatment. The cluster B include 14 genotypes grouped together with GP < 80 % (i.e. Pradhan Dhan, Adira 3, Pandya, etc). Cluster C constitutes six genotypes with GP % more than 90 % and moderate vigour indicating a relatively better response to high-temperature conditions. Those in cluster D (Adira 1, Adira 2 and Marathondi) appear to be most stable and heat tolerant with high GP (more than 80 %), SOG, SL (> 12cm) and very high vigour among the genotypes. Clusters E and F include genotypes that could not withstand variable temperature conditions showing very low GP (< 30 %). Overall, the cluster analysis, along with principal component analysis (PCA), provides a clear understanding of genotype responses to high-temperature stress (26). Clustering helped to identify the group of

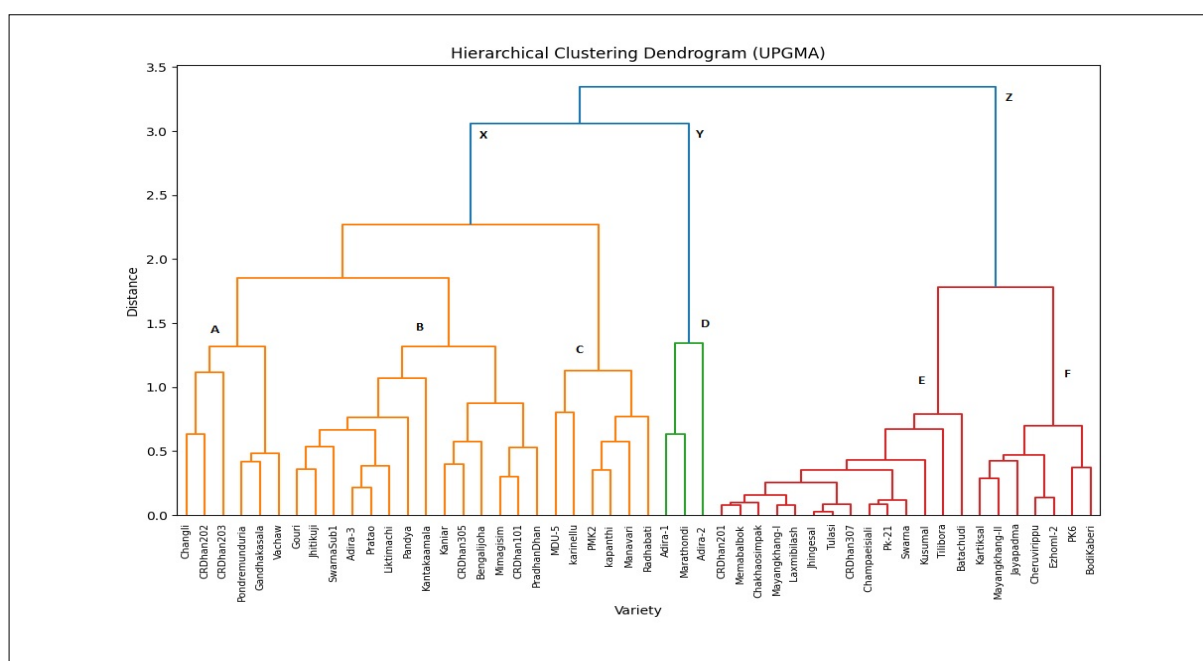
genotypes that are stable under variable temperature conditions. These groups can likely be used appropriately for the development of stable and heat tolerant rice varieties in the future.

The biplot visualises the results of PCA on the rice dataset (Fig. 5), which shows the relationships between 50 rice varieties and four statistical features ('GP', 'SOG', 'SL', 'SV-I'). In the biplot each point represents a rice variety, which is projected onto a plane based on the first two principal components (PC1 and PC2). These two PCs explain the maximum variance. The arrows represent the loading vectors of the variables, where their direction and length indicate the magnitude and contribution of each trait to the principal components.

The angle between the feature arrows indicates the relationship between them. If the arrows point in the same direction, they are positively related, while if they are in the opposite direction, they are negatively related. If there is a  $90^\circ$  angle between two features, they are considered to be unrelated. The length of an arrow indicates the strength of its influence a longer length means the feature explains more variance. The position of the dots relative to the arrows indicates the feature value of that rice type. If a dot is in the direction of an arrow, that rice grain has a high value for that feature and if it is in the opposite direction, it has a low value. If the position is far from the origin, that rice grain is an outlier or very diverse. This plot shows the clustering of rice varieties, which means that some rice varieties have similar features. These clusters can be identified and used in breeding and quality control. Overall, this plot makes it easy to understand the deep relationships between rice varieties and multivariate data, serving as a visual tool to understand patterns and outliers.

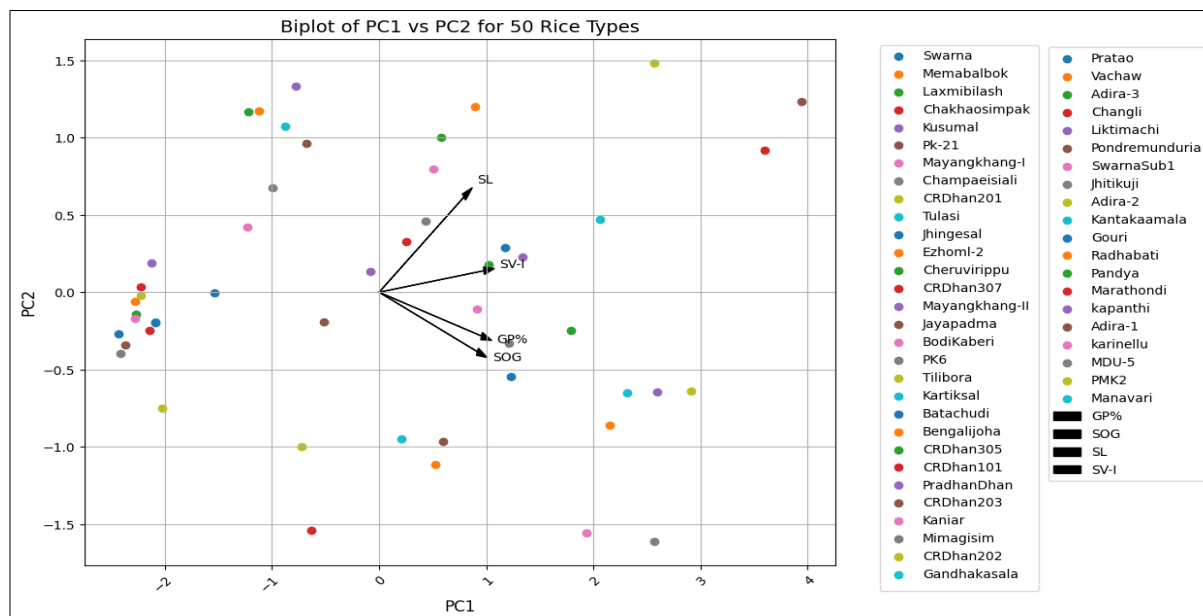
The GP and SOG arrows point in the same direction, indicating a strong positive relationship between these two traits and mainly explain PC1. The SL and SV-I are more influential in PC2. Rice genotypes that are in the direction of these arrows have higher values for that trait and those that are in the opposite direction have lower values for that trait.

The PCA screen plot (Fig. 6a) visualises the proportion of



**Fig. 4.** Dendrogram of 50 rice genotypes under variable temperature conditions.

UPGMA : unweighted pair group method with arithmetic mean.



**Fig. 5.** Principal component analysis for seed quality traits of 50 rice genotypes under variable temperature conditions.

GP: germination percentage; SOG: speed of germination; SL: shoot length; SV-1: seedling vigour index-1

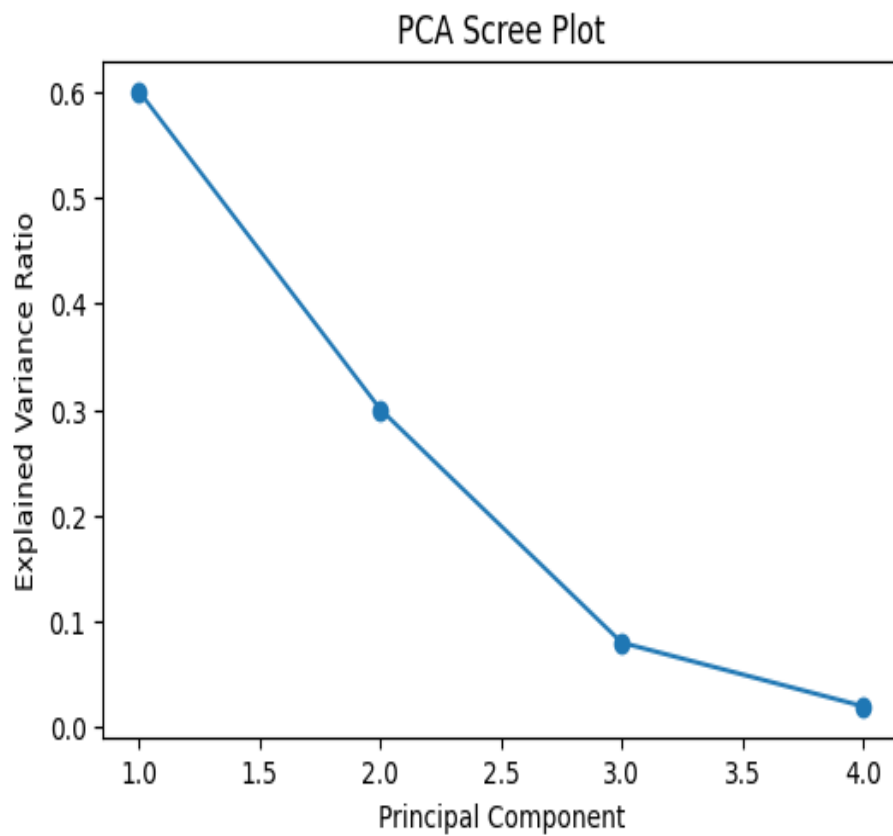
variance explained by each of the four principal components derived from the dataset. The first principal component accounts for the highest variance, approximately 60 %, indicating it captures the most significant patterns in the data. The second component explains around 30 %, cumulatively covering about 90 % of the total variance when combined with the first. The third and fourth components contribute only marginally, around 8 % and 2 % respectively, suggesting they add limited new information. The steep decline from PC1 to PC2 followed by a gentler slope in subsequent components implies diminishing returns in explanatory power. This pattern supports the selection of the first two components for dimensionality reduction without substantial loss of information. Such a reduction can simplify data visualisation and modelling while retaining the essential variance structure. The clear dominance of the first two components reflects strong correlations among original variables. Similar analysis was also performed by previous researchers and found crucial for this study (27). Thus, this PCA analysis effectively highlights that most of the variability in seed quality traits under control and stress conditions can be explained in a lower-dimensional space.

The PCA score plot (Fig. 6b) presents a two-dimensional representation of the dataset using the first two principal components, which together explain a significant portion of the variance. Each point in the plot represents an observation projected onto this reduced space, with colours indicating cluster membership. Three clusters, labelled 0, 1 and 2, are shown in different colours, suggesting some degree of separation in the data structure. While the clusters are not tightly grouped, moderate patterns of grouping can be observed, particularly for cluster 2 (yellow), which is somewhat distinct across the plot. The overlapping regions among clusters 0 (purple) and 1 (green) suggests partial similarity or shared characteristics among those data points. This visualisation confirms that PCA has effectively reduced the dimensionality, allowing for easier interpretation and visual detection of structure. However, the dispersion also indicates that clustering might benefit from further refinement, perhaps through deeper analysis or alternative clustering methods. Overall, the PCA score plot offers useful insights into the data's intrinsic structure and variability within and between clusters (25).

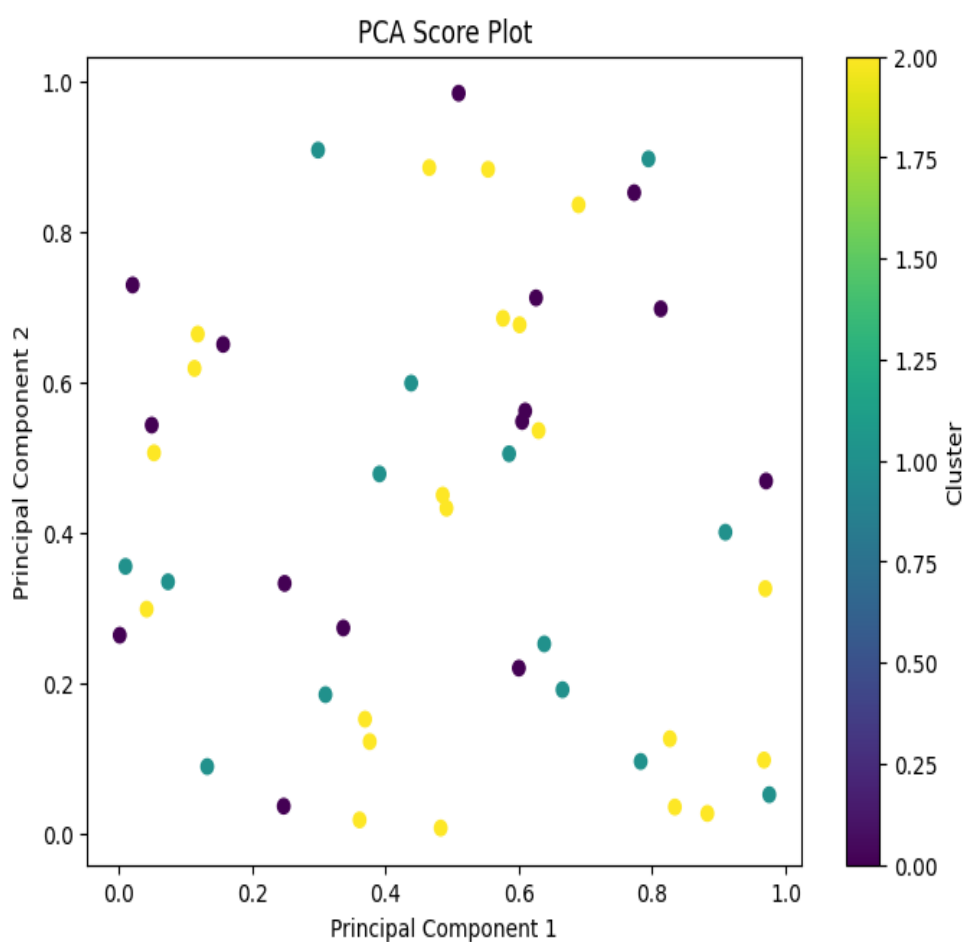
The effect of high temperature on SOG and SV-I is significantly detrimental (Fig. 7a). These two traits showed 76.51 % and 75.51 % change respectively. The SL has changed by 57.40 %, indicating a moderate effect and GP has changed by 52.05 %, indicating that this trait is less affected by high temperature than other traits. This may be because growth and vigour are affected first decreasing the performance of the seed followed by effect on viability (GP). This study shows that speed of germination (SOG) and seedling vigour (SV-I) are the most sensitive traits to high temperature which was also confirmed by previous researchers (28). Studies (28, 29) also reported a significant decrease in germination percentage, root length, shoot length and other related parameters under elevated temperature and moisture conditions, primarily due to the loss of seed membrane integrity and denaturation of essential proteins (8). Among the fifty rice genotypes as shown in Fig. 7b, the effect of variable temperature was maximum in Changli, Tilibora, CR Dhan307, Champaisiali, PK21 and Swarna which may be the result of accumulation of reactive oxygen species (ROS) and disruption of essential enzymatic functions (8–10). The least effect was seen in Kantakamala, MDU-5, Bengaliyoha, Liktimachi, Pratao etc. The genotypes having good performance under the treatment can be used in crop improvement programmes in future study for development of climate resilient genotypes.

## Conclusion

The current research states that the application of variable temperature regimes (long ambient storing and then exposure to high temperature) causes an acceleration of seed deterioration in rice. Thermal stress negatively influenced all the seed quality characteristics with speed of germination and seed vigour index being the most sensitive to thermal stress followed by seedling length and germination percentage. The high positive relationships between the parameters of germination, vigour and seedling growth reveal their interdependence and joint effect on seed longevity. Multivariate data analysis such as cluster and principal component analysis was useful in identifying the genotypes of rice depending on ageing effects of temperature, which demonstrated genetic variability of seed longevity under

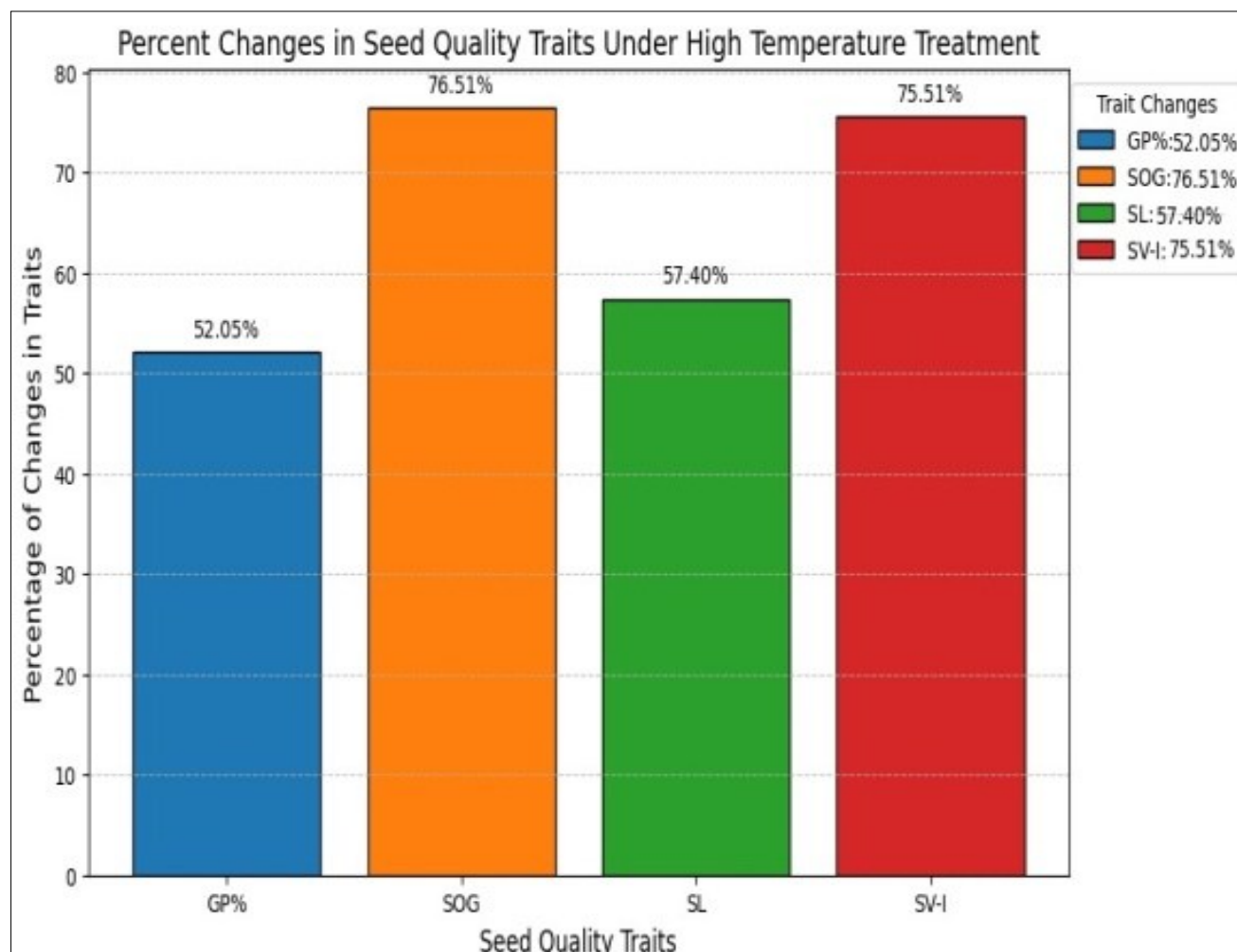


(a)

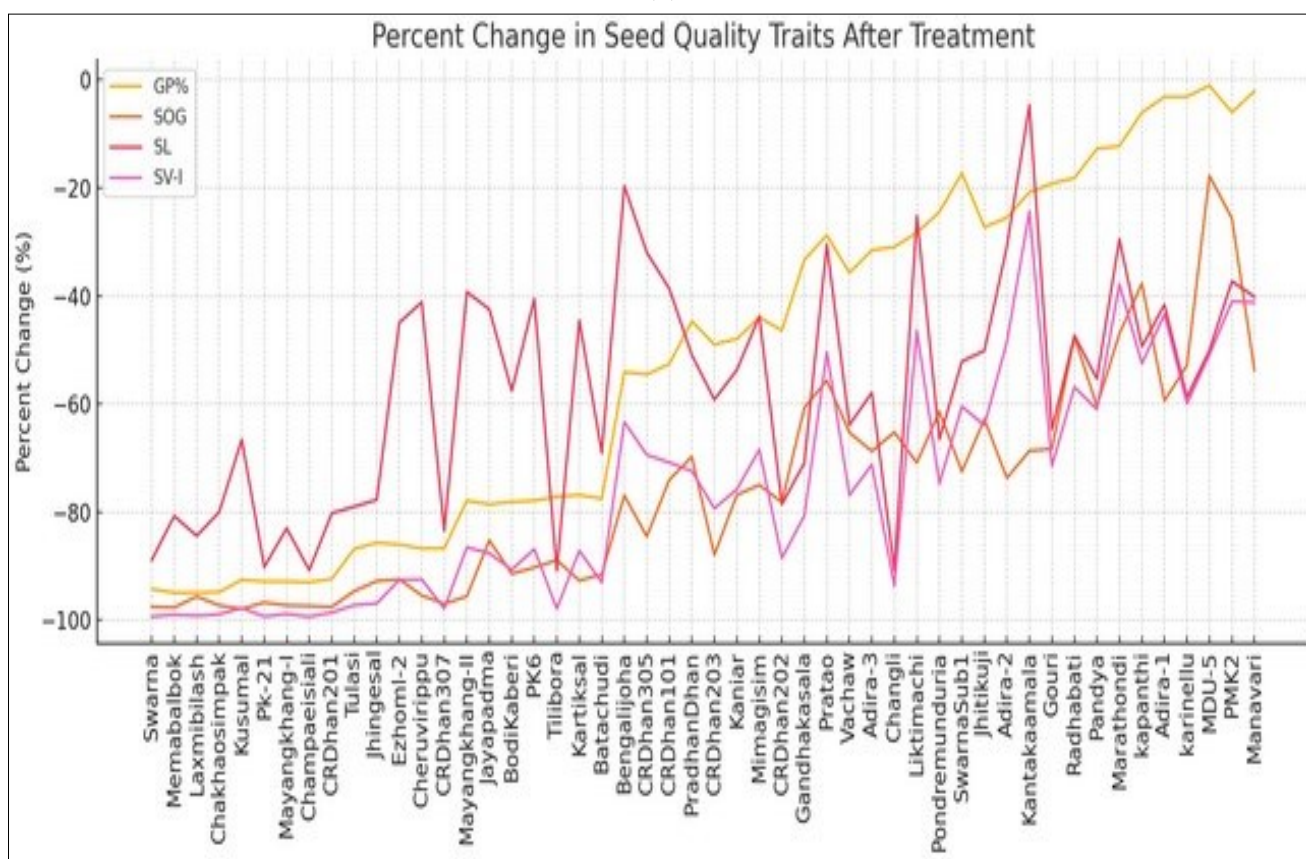


(b)

**Fig. 6.** Principal component analysis. a: scree plot; b: score plot; PC: principal component; PCA: principal component analysis



(a)



(b)

**Fig. 7.** (a) Effect of high temperature in seed quality traits; (b) Percent change in seed quality traits for 50 rice germplasm lines.

stress. The genotypes that were mostly tolerant to stress associated with variable temperature conditions included MDU-5, Manavari, Radhabati and PMK-2. They showed a high level of seed viability and vigour in comparison with other genotypes susceptible to the stress. The findings highlight the need to assess the seed longevity in real climatic conditions by taking into account temperature changes and storage conditions, when analysing the longevity of seeds. The tolerant genotypes that have been identified can be of great use as donor lines in breeding programmes to come up with climate-resistant rice varieties with better seed storability. Moreover, the research offers a scientific foundation on how seed storage policies and strategies should be refined to overcome the negative impact of increase in temperature due to the varying climatic conditions.

## Acknowledgements

We extend our thanks to all the lab mates for their help in data collection and assistance in manuscript preparation.

## Authors' contributions

SKP and PS suggested a blueprint of the research, allocated resources and actively associated with research problems as well as data collection. They also contributed to the preparation and scrutinisation of the manuscript. SS carried out the field and lab work. SM, JM, DL, MD and SKT performed the graphical representation of the data and assisted in data compilation. NB, GK and SSS contributed to the experimental design and assisted in data 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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