



RESEARCH ARTICLE

Determining physiological maturity for optimal seed quality and reduced yield loss in foxtail millet (*Setaria italica* (L.) P. Beauv.)

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Abstract

The present study aimed to determine the right stage of physiological maturity (PM) in foxtail millet cultivars ('Suryanandi' and 'SiA 3156') during two post-rainy seasons. The seed formation/developmental phase required about one week after flowering in year 1 and two weeks in year 2 in both cultivars, due to varying climatic parameters. The maturation of seeds progressed gradually, with a loss in moisture and gain in hardness, test weight and seed yield, during subsequent harvests at weekly intervals, which continued until 35 days after anthesis (DAA) (year 1) and 42 DAA (year 2) in both cultivars. The seed quality traits reached their maximum at 35 DAA during year 1 and thereafter declined gradually; the decline was more prominent in the case of aged seeds, indicating that seed viability would be lost faster due to delayed harvests. During year 2, the seed quality traits were at their maximum in the harvest at 42 DAA. Due to significant reduction in quality traits at a faster rate at later stages of harvest, the polynomial regression analysis predicted maximum quality of seeds at 38 DAA. The study found that the seeds reached the right stage of PM at 35 DAA in the year 1 and at 38 DAA during year 2 in both cultivars, providing valuable insights that PM generally occurs between 35 and 38 DAA, while the optimal harvest window is between 35 and 42 DAA during the post-rainy season in foxtail millet. At PM, the panicles turn brown, the seeds become hard, shiny, pale-yellow with elliptic streaks and a dark-brown depression develops at the hilar end and these act as visual indicators for the optimal time of harvest in foxtail millet.

Keywords: foxtail millet; physiological maturity; polynomial regression; seed quality; seed yield; visual indicators

Introduction

Foxtail millet (*Setaria italica* (L.) P. Beauv.) cultivation dates back more than 10500 years to China (1). It is a member of the family Poaceae, subfamily Panicoideae and tribe Paniceae, with a chromosome number of $2n = 18$ (AA). Foxtail millet matures in 60-90 days, making it a short duration crop for food, feed and fodder. It can be successfully cultivated in semi-arid areas with low precipitation and at altitudes from sea level up to 2000 m above mean sea level. It is one of the most resilient cereal crops, being fairly tolerant to drought and can escape late season droughts because of its short growing period. The dehusked grains are rich in protein (12.3 %) and fibre (8.0 %) content and have a low glycemic index (GI) due to slow digestibility, which makes them suitable as a diabetic food to regulate blood glucose levels (2, 3). Furthermore, it is beneficial for the prevention of cardiovascular diseases (4).

Foxtail millet is estimated to be cultivated in around 1.06 m ha globally (IIMR estimates based on FAO/DES-GOI data) with a production of 2.29 m tonnes. China produced about 1.81 m t of grains from an area of 0.72 m ha with a yield of 2519 kg/ha in 2014 (5). In India, foxtail millet is presently cultivated on a very limited area to meet domestic needs in the states of Andhra Pradesh,

Karnataka and Tamil Nadu and some north-eastern regions.

In any seed production programme of a crop, identification of proper stage of seed maturity and right stage of crop harvest is very important as the resultant seed quality decides the proper establishment of subsequent crop. A series of events occur in a sequential order during seed development and maturation process, including embryogenesis, morphogenesis and accumulation of food reserves. The advancement of maturation process can be gauged through relative changes in seed hardness, moisture content, test weight, seed germination, vigour and viability potential (6, 7). The end of seed filling period is considered as PM and at this point, the seed quality is the highest and declines thereafter (8). Beyond the stage of PM, the agronomic interventions cannot increase seed yield, due to the loss of funicular functionality and the cessation of nutrient supply from mother plant to seed (9). PM is the seed developmental stage at which a seed or the majority of a seed population, reaches to maximum vigour and viability and it is also the point of maximum seed quality (10, 11). The determination of exact stage of seed maturity using different traits has been reported in different crops based on seed dry weight and moisture content, seed germination

traits, accelerated aging and electrical conductivity, respiratory enzymes and mobilization of reserves (12-17).

Apart from seed quality in crops like foxtail millet, shattering of seeds is a major problem during delayed harvest, which leads to reduced seed yield as well as deterioration in the field due to exposure to adverse environmental factors. Low quality seeds lead to a decrease in germination and seedling emergence, which results in poor crop stand establishment and subsequent yield loss in the field. Knowledge on seed maturity patterns and their influence on seed vigour, viability and yield traits is scanty in foxtail millet. Hence, it is important to understand these factors to overcome the problems arising from varying seasonal climatic parameters during seed production. The determination of right stage of PM and identification of suitable harvestable maturity (HM) of seeds are fundamental prerequisites for eliminating seed deterioration in the field and consequent loss of productivity and seed quality. Therefore, the present study aimed to determine the appropriate stage of PM and right stage of HM in foxtail millet to minimize the losses in seed yield and quality during seed production.

Materials and Methods

Experimental site, materials and design

The experiments were conducted during the late post-rainy seasons at ICAR-Indian Institute of Millets Research in Hyderabad, India, located at 17.3850° N, 78.4867° E and an altitude of 505 m above MSL. The sowings took place on January 7, 2019 (year 1) and December 13, 2019 (year 2), using a randomized complete block design (RCBD) with three replications. Two popular cultivars Suryanandi and SiA 3156 of foxtail millet were procured from PC unit-AICRP on small millets. Suryanandi is a pure line selection released in 2012 for cultivation in the state of Andhra Pradesh with average yield of 20 to 25 q/ha. SiA 3156 is also a pure line selection released in 2024 for all states of India with an average yield of 20 to 25 q/ha. The earliest date of appearance of seed setting (7 DAA in year 1 and 14 DAA in year 2) was identified as the first stage of harvest (HS I) and eight subsequent harvests (HS I to HS VIII) were made at weekly intervals for both cultivars (Table 1).

Seed yield, moisture content, hardness and test weight

The seed weight per plant was measured from five randomly labelled plants at each harvest stage and recorded in grams (g). The seed yield per net plot (6 m²) of every 100 plants was calculated and expressed in grams (g). Fresh seed samples were collected at each harvest stage and evaluated for moisture content using a digital seed moisture meter (*FARMEX-MT-PRO*, *FARMCOMP*, *Agro-electronics, USA*), calibrated specifically for millet seeds. The moisture content values were expressed as a percentage. Seed hardness was measured using a digital hardness tester (Pharmag Instruments Ltd., India), which operates with a force gauge to apply tension or compression to a single seed. The hardness of ten randomly selected seeds from each replication (four replicates per sample) was tested and the mean value was reported in kilogram force (kgf). For test weight determination, four replicates of 100 seeds from each

sample were counted and weighed in milligrams (mg).

Seed germination and vigour traits

The seed germination tests were carried out following the guidelines set by the International Seed Testing Association (ISTA) for foxtail millet (18). Germination counts were taken on the 10th day and the seedlings were assessed for growth and vigour characteristics. The germination percentage (G) was calculated based on the number of normal seedlings produced per 100 seeds. Ten normal seedlings were randomly selected to measure seedling traits. Root length (RL) was measured from the collar region to the tip of the primary root, while shoot length (SL) was recorded from the collar region to the tip of the first leaf. Seedlings with abnormal growth were discarded. Seedling dry weight (SDW) was determined by drying the ten selected seedlings in a hot air oven at 80 °C for 24 hr. After drying, the seedlings were placed in a desiccator for 30 min to cool and their mean dry weight was measured. Seedling vigour indices were calculated using the following formulae: Seedling vigour index-I (SVI-I) = {seed germination (%) × seedling length (cm)}; Seedling vigour index-II (SVI-II) = {germination (%) × seedling dry weight (g)}. Field emergence (FE) was tested for both fresh and accelerated-aged seeds by sowing 50 seeds per replication in four replications. The seeds were planted in cement pots (45 cm diameter) filled with a soil mixture of red and black soils in appropriate proportions. After 20 days, the number of seedlings with leaves above the soil surface was counted and expressed as a percentage.

Seed storability

The accelerated ageing (AA) test for seed was conducted in an ageing chamber (Memmert-HPP 108/749, Germany) (19). The sampled seeds from each stage of maturation were subjected to accelerated ageing. The seeds in a single layer were placed on stainless steel mesh racks inside the ageing chamber to create a higher humidity of 90 % at 44 ± 1 °C during the test for required periods (as identified with prior standardization) specific to foxtail millet.

α-amylase enzyme activity in seedling

Dry seeds weighing 0.2 g were allowed to germinate in petri-plates with moistened filter paper. The samples were harvested on the 3rd, 5th and 10th days of germination. The samples, in triplicates, were used to estimate the α-amylase activity, assayed according to earlier reported procedure (20). The α-amylase activity was expressed as the number of micromoles of maltose released per minute by total enzyme extract from 100 seeds (after converting sample weight into number of seeds using test weight of respective harvest stages) (μmol. min⁻¹. 100 seeds⁻¹).

Electrical conductivity test

One gram of seed from each harvest was weighed and then immersed in 100 mL deionized water at 25 °C for 24 hr. The electrical conductivity of leachates for four replicates was measured using a conductivity meter (Systronics Model 306, India) and conductivity per gram of seed weight was calculated (μS.cm⁻¹.g⁻¹) and recorded.

Table 1. Mean number of days required after anthesis for harvest stages at equal intervals after stage-I (at visibility of seed setting) to stage-VIII (at visibility of over-matured seeds) in foxtail millet cultivars Suryanandi and SiA 3156

Harvest stages (HS)	Days after anthesis (DAA)							
	I	II	III	IV	V	VI	VII	VIII
Year 1	7	14	21	28	35	42	49	56
Year 2	14	21	28	35	42	49	56	63

Statistical analysis

The data were transformed into arc-sine values wherever necessary and ANOVA was performed in a RCBD using a statistical software package (Statistix, version 8.1). The polynomial regression model, adjusted to the second order (degree), was applied to predict the right stage of harvests to obtain maximal seed yield, vigour and storability traits.

Results and Discussion

Seed moisture content and hardness

Completion of anthesis required 64 days after sowing (DAS) in foxtail millet cultivars Suryanandi and SiA 3156 during both seasons of experimentation. The seed developmental phase required about one week (7 DAA) in year 1 and two weeks (14 DAA) in year 2 in both the cultivars, indicating a varying physiological response for seed setting under different climatic conditions across years (Fig. 1). The first stage of harvest (HS-I), however, resulted in immature seeds, mostly with high moisture content. The maturation of seeds progressed gradually with a loss of seed moisture and a gain in seed hardness and test weight, considerably during subsequent harvests at weekly intervals, which continued until maximum dry matter accumulation i.e. the probable stage of PM at 35 DAA (year 1) and 42 DAA (year 2) in both cultivars (Fig. 2a-d). At the time of transition from seed development to maturation phase, a series of cell divisions and cell differentiations occur, which differ between early reserve accumulation and late maturation drying. Seed acquires desiccation tolerance during early maturation and the mechanisms behind the onset of desiccation tolerance are activated in orthodox seeds (21). Sequential changes occur in the seed from fertilization until the seed turns independent from the mother plant due to cessation of nutrient supply (22). Technically, the matured seed exhibits sufficient moisture, maximum dry matter, high germination and vigour (6, 7, 22, 23).

Seed test weight and yield

The seed test weight, seed yield per plant and plot reached maximum levels at 35 DAA and thereafter declined significantly during year 1 (Fig. 2a, b). In contrast, during year 2, seed test weight continued to increase significantly even after 35 DAA and reached

maximum at 42 DAA (Fig. 2c, d). The seed yield per plant in cv. Suryanandi was on par between 35 and 42 DAA, however, the per-plot yield recorded significant reduction. Whereas in case of cv. SiA 3156, seed yield per plant reduced significantly from 35 to 42 DAA, but the reduction was on par with yield per plot. In foxtail millet, the seeds are delicately attached in panicles at maturity, which leads to faster and irregular shattering of seeds among the plant population, causing a reduction of seed yield. However, the level of shattering differs between cultivars and hence the variation in seed yield was observed in two cultivars at 42 DAA. Late harvests lead to loss in seed yield due to shattering, damage to seed and the risk of rain, which results in poor-quality seeds (6, 7, 24).

A polynomial regression model was applied to predict the seed yield, which indicated the highest yield at 35 DAA in cv. Suryanandi ($R^2 = 0.716$) and cv. SiA 3156 ($R^2 = 0.816$) during year 1 (Fig. 2e). However, the polynomial regression for year 2 revealed maximum yield per plant at 38 DAA in cv. Suryanandi ($R^2 = 0.933$) and cv. SiA 3156 ($R^2 = 0.852$) (Fig. 2f). Maximum dry matter accumulation in the seed is an indicator of PM, whereas the end of seed filling phase is termed as mass maturity (8, 25, 26). At this stage, the panicles of foxtail millet turn brown and the seeds became hard, shiny, pale-yellow, with elliptic streaks (Fig. 3a-e). When the seed coat was removed at maturity, a marked layer of dark-brown depression was found at the hilum end of the seed (Fig. 3f). These visual signs could serve as morphological indicators of seed physiological and harvestable maturity in foxtail millet, as reported in other crops like sorghum, barnyard millet and kodo millet (6, 7, 27, 28).

Seed quality and storability

Inadequate development of essential structures and protection mechanisms in early harvests leads to poor quality of seeds, whereas during late stages of seed maturation, the protection mechanisms are fully developed; therefore, the identification of the proper stage of harvest remains critical for seed quality and storability (29-31). In the present study, with the progress of seed maturation in the field, the seed quality traits viz. germination, field emergence and seedling vigour of fresh seeds increased steadily (Fig. 4a-f). The seed quality traits reached a maximum at 35 DAA during year 1 and thereafter declined gradually, with the decline was more prominent in aged seeds, indicating that seed viability would be lost faster due to delay in harvest after 35 DAA in foxtail millet (Fig. 4a-d). However, during year 2, the seed quality traits were maximum with the harvest at 42 DAA, though on par with 35

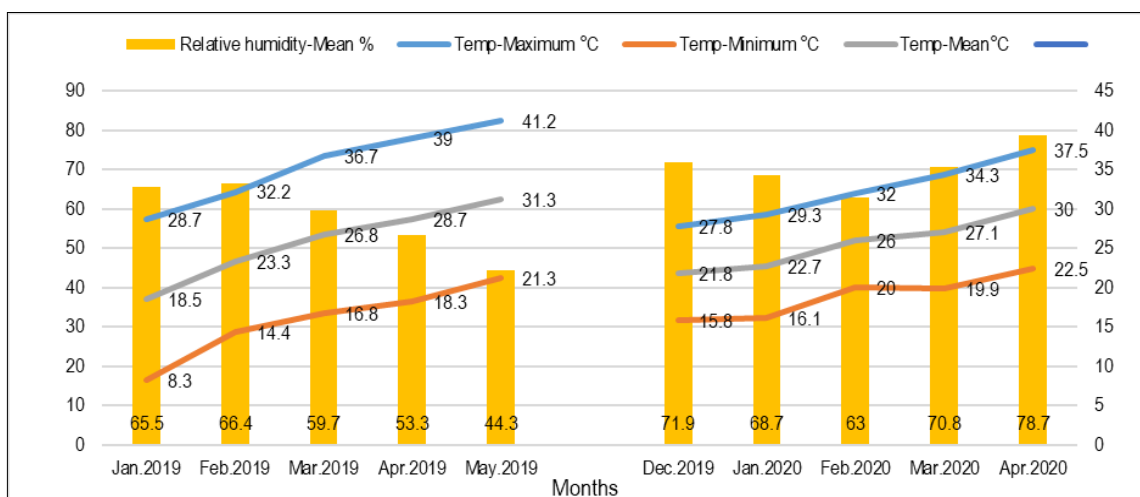
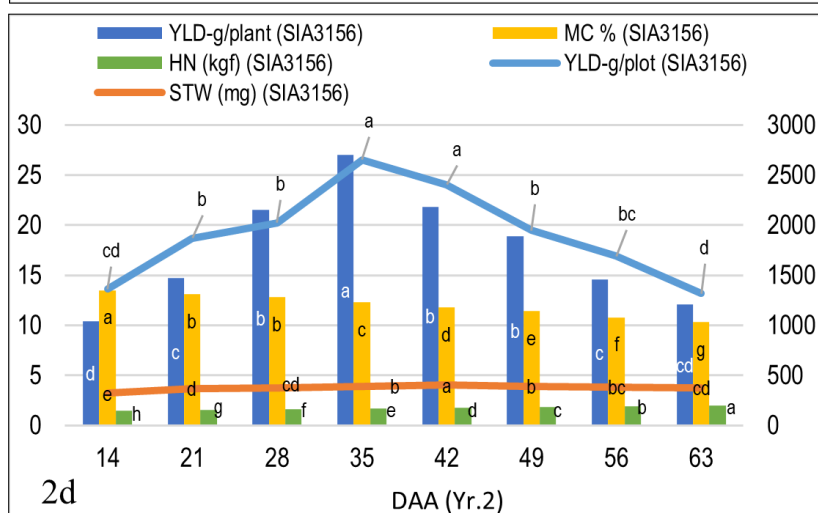
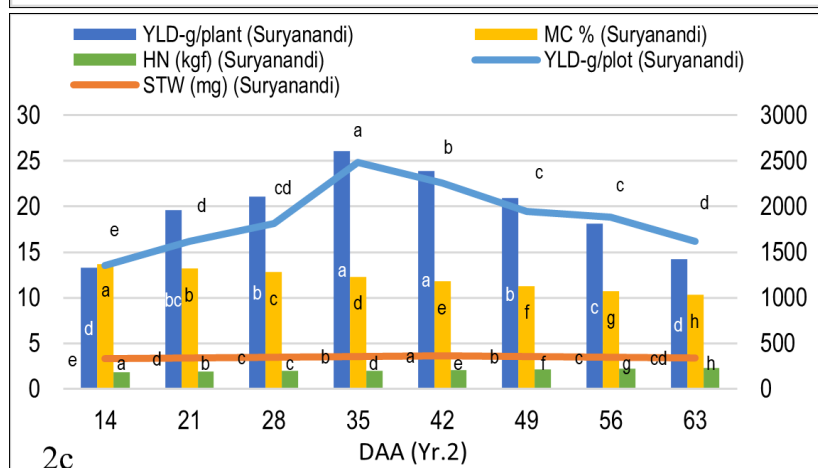
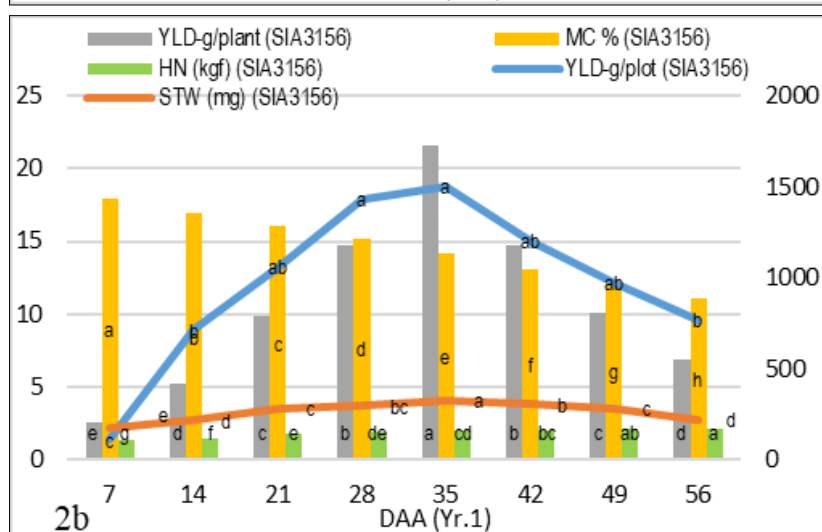
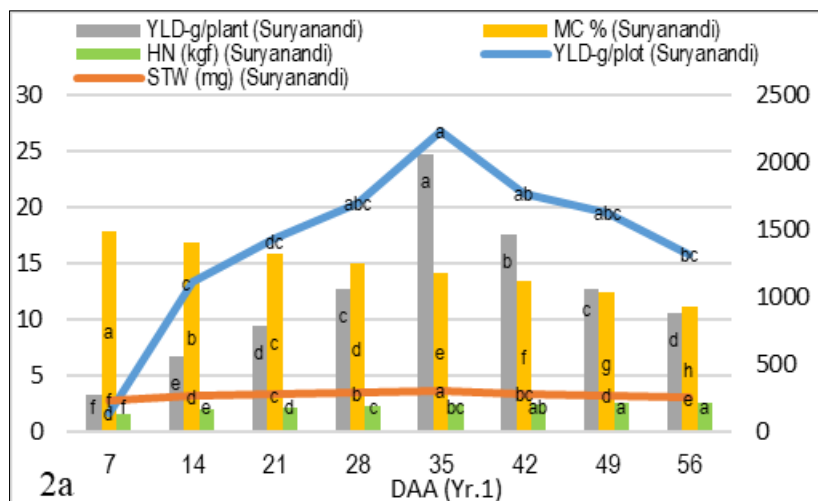


Fig. 1. Temperature and relative humidity during two post-rainy seasons (January to May 2019 and December 2019 to April 2020) at Hyderabad, India.



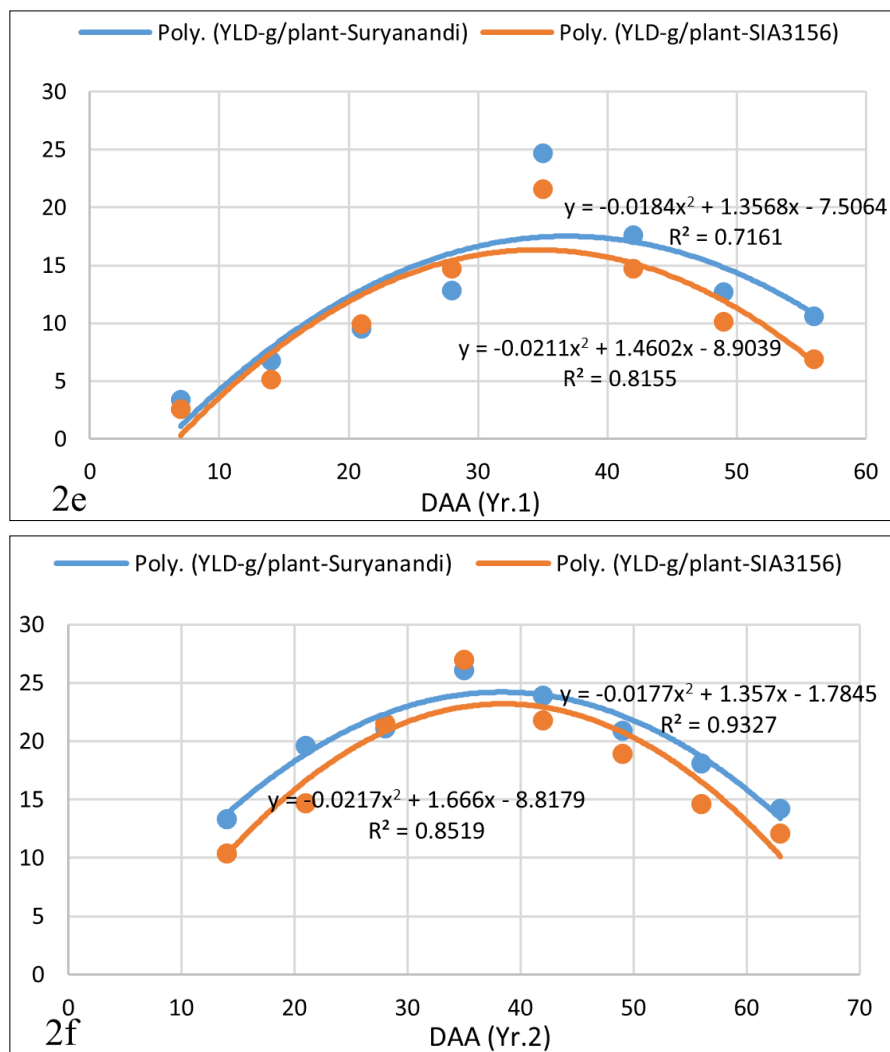


Fig. 2a-d. Effect of different stages of harvest (DAA) on yield (YLD), moisture content (MC), hardness (HN) and test weight (STW) of fresh seeds during year 1 (Yr. 1) and year 2 (Yr. 2) in foxtail millet. The mean data with different labels (a, b, etc.) indicate significant differences as per Tukeys HSD all pairwise comparison test. **e, f.** Polynomial regression analysis for seed yield traits against days after anthesis (DAA) during year 1 (Yr.1) and year 2 (Yr.2) in foxtail millet.

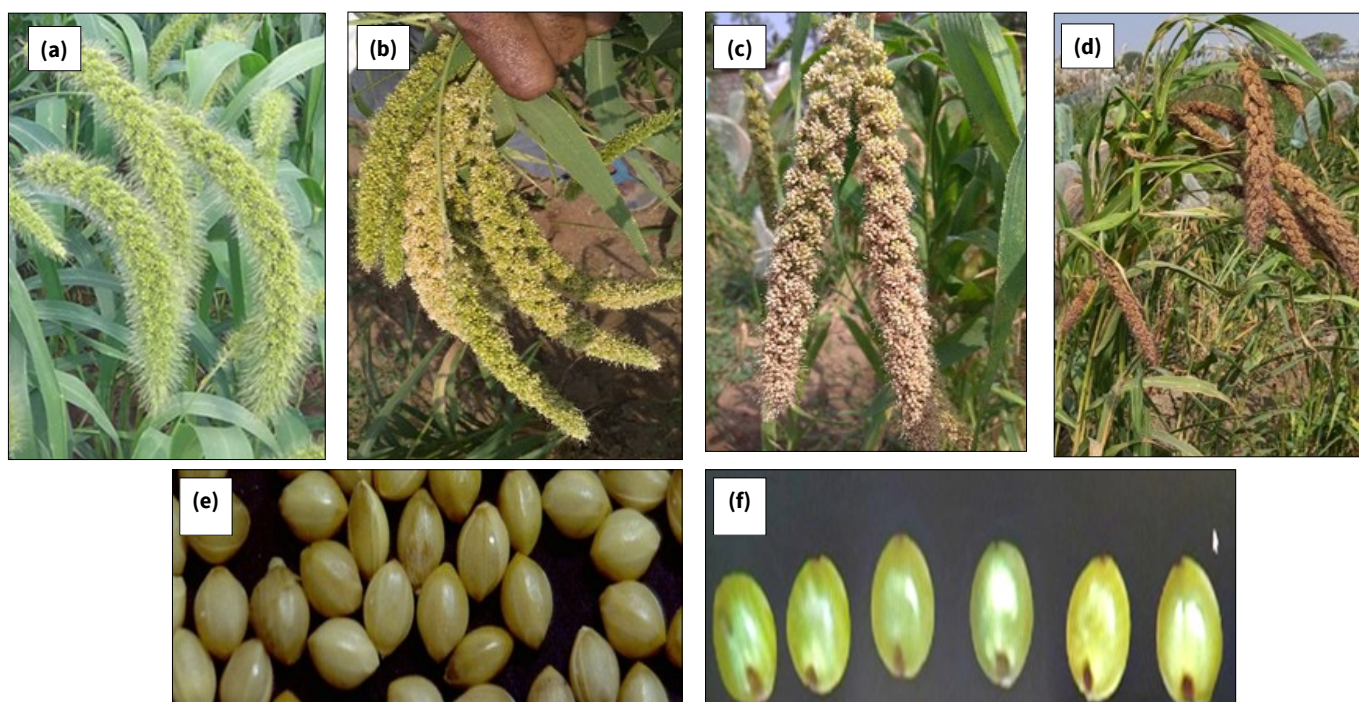
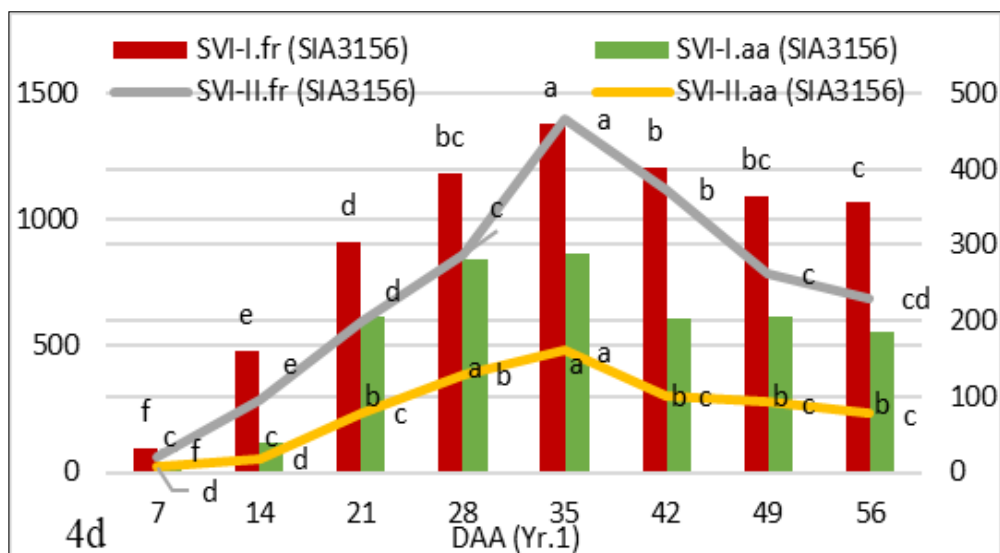
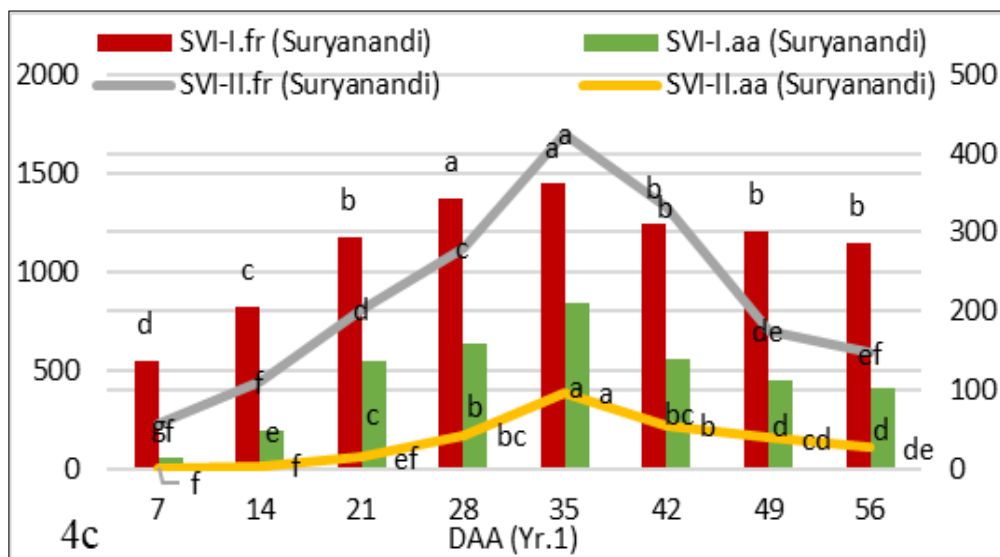
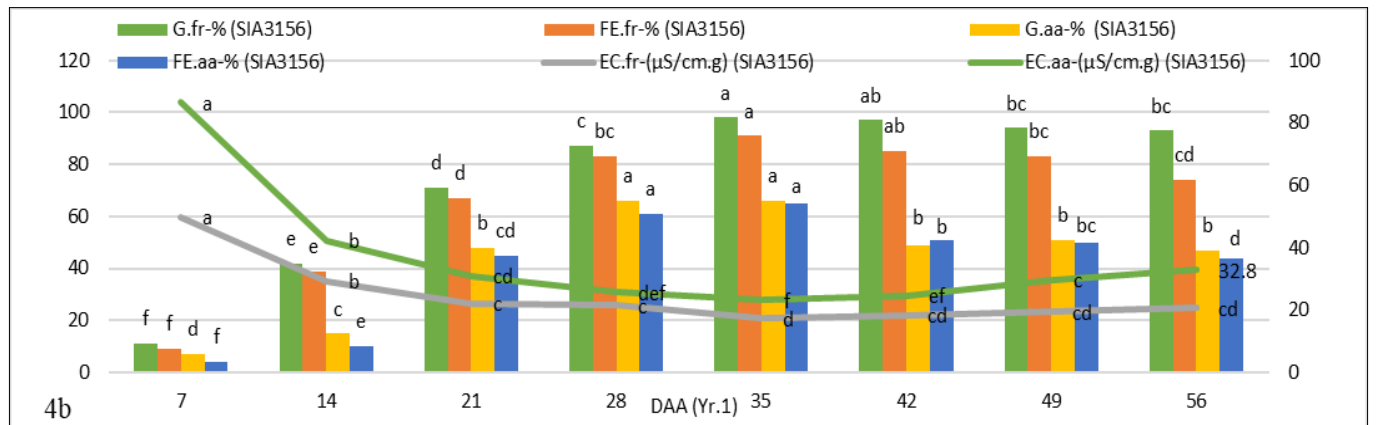
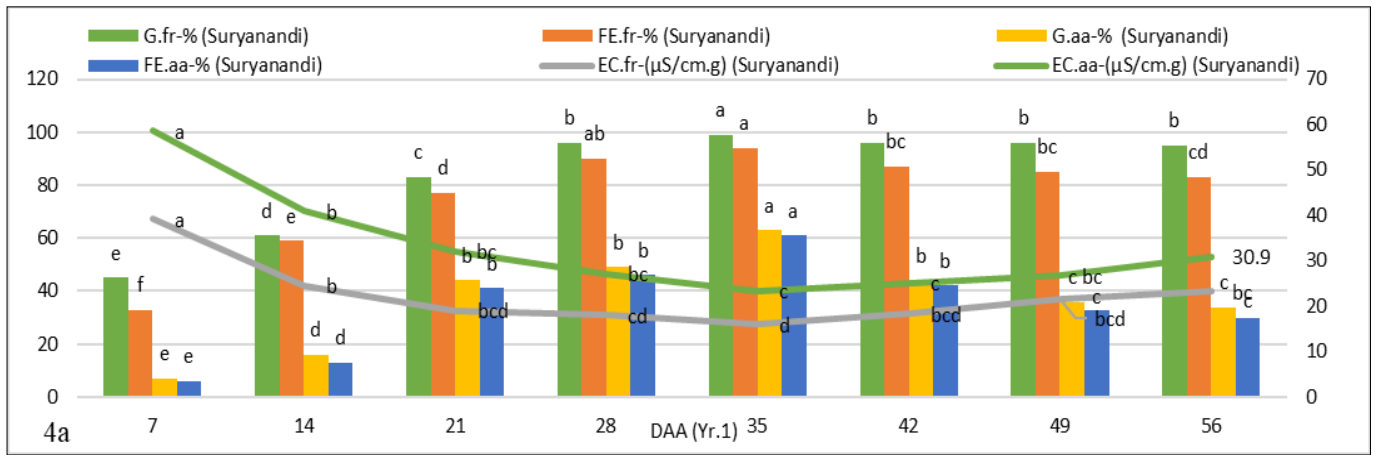


Fig. 3. Appearance of foxtail millet panicles and seeds at different stages of seed development and maturation. **a.** Panicle at flowering stage, **b.** Initial stage of seed maturation in panicles, **c.** Seed maturation progressing from tip towards bottom of the panicles, **d.** Appearance of panicles at maturity stage with most of the panicles in brown colour, **e.** Seeds become hard and shiny with pale-yellow patches and projected streaks at maturity, **f.** When seed coat is removed at maturity, a depression in dark-brown colour appear at hilum end of seed.



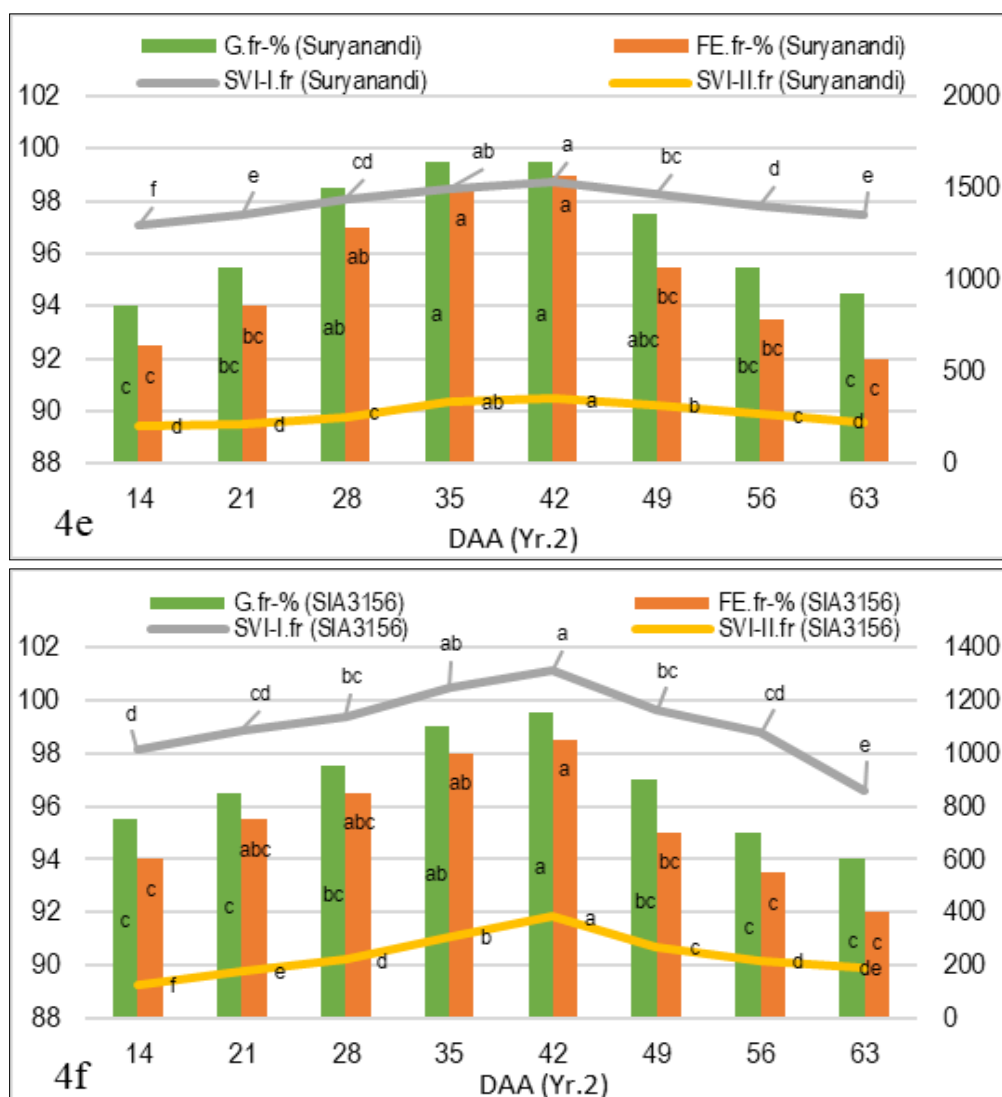


Fig. 4a-f. Effect of different stages of seed harvest (DAA) on seed germination, field emergence and electrical conductivity and seedling vigour index of fresh and aged seeds in year 1 (a-d) and year 2 (e-f) in foxtail millet. G.fr %: germination of fresh seeds, G.aa %: germination of aged seeds, SVI.fr: seedling vigour index of fresh seeds, SVI.aa: seedling vigour index of aged seeds, FE.fr %: field emergence of fresh seeds, FE.aa %: field emergence of aged seeds, EC.fr-($\mu\text{S}/\text{cm}/\text{g}$): Electrical conductivity of fresh seeds, EC.aa-($\mu\text{S}/\text{cm}/\text{g}$): Electrical conductivity of aged seeds, Yr.1: Year 1, Yr.2: Year 2, DAA: days after anthesis. The mean data with different labels (a, b, etc.) indicate significant differences as per Tukeys HSD all pairwise comparison test.

DAA for these traits (Fig. 4e, f). After 42 DAA, seed germination, field emergence and seedling vigour traits decreased significantly.

The predictions based on polynomial regression indicated that the seed germination and seedling vigour of fresh (fr) and aged (aa) seeds were highest at 35 DAA during year 1 ($R^2 = 0.97$ for G.fr %, 0.86 for G.aa %, 0.94 for SVI-I.fr, 0.86 for SVI-I.aa in cv. Suryanandi; and $R^2 = 0.99$ for G.fr %, 0.86 for G.aa %, 0.96 for SVI-I.fr, 0.84 for SVI-I.aa in cv. SIA3156) (Fig. 5a, c). However, during year 2 the regression model predicted maximum germination and seedling vigour of fresh seeds at 38 DAA ($R^2 = 0.91$ for G.fr %, 0.94 for SVI-I.fr in cv. Suryanandi; and $R^2 = 0.86$ for G.fr %, 0.89 for SVI-I.fr in cv. SIA3156) (Fig. 5b, d).

At PM, most of the seeds exhibit maximum vigour and viability and it is the point of maximum seed quality (10, 11). During year 1, the maximum temperatures recorded during harvest stages were 2 °C higher than year 2, whereas the minimum temperatures were lower than those in the later year (Fig. 1). The growing degree-days (GDD) of heat energy accumulation determine plant growth, development and PM (32, 33). From these results it is evident that foxtail millet seeds are more prone to field

weather conditions and even a week delay in harvest leads to significant loss of quality, particularly the seed storability. This is due to the exposure of overmatured seeds to varied weather conditions, particularly temperature, which contributes to a decline in seed vigour and viability (34-36). The high temperatures and drought during anthesis and seed development stages affect the seed quality due to deterioration (37, 38). The exposure of seeds to unfavorable weather conditions due to delayed harvest leads to the deterioration of seeds in field itself (39).

Membrane integrity and leakage of electrolytes

During seed deterioration, loss of membrane integrity is the primary physiological event as indicated by electrical conductivity (EC) test (19). During year 1, the EC ($\mu\text{S}/\text{cm}/\text{g}$) values of fresh and aged seeds harvested at weekly intervals showed higher values at initial stage of harvest, then decreased significantly until 35 DAA and subsequently rose gradually with delayed harvests (Fig. 4a, b). Due to desiccation, immature seeds are more prone to electrolyte leakage during the initial germination process (40). Comparatively, the aged (aa) seeds recorded higher EC values than fresh seeds at all harvest stages

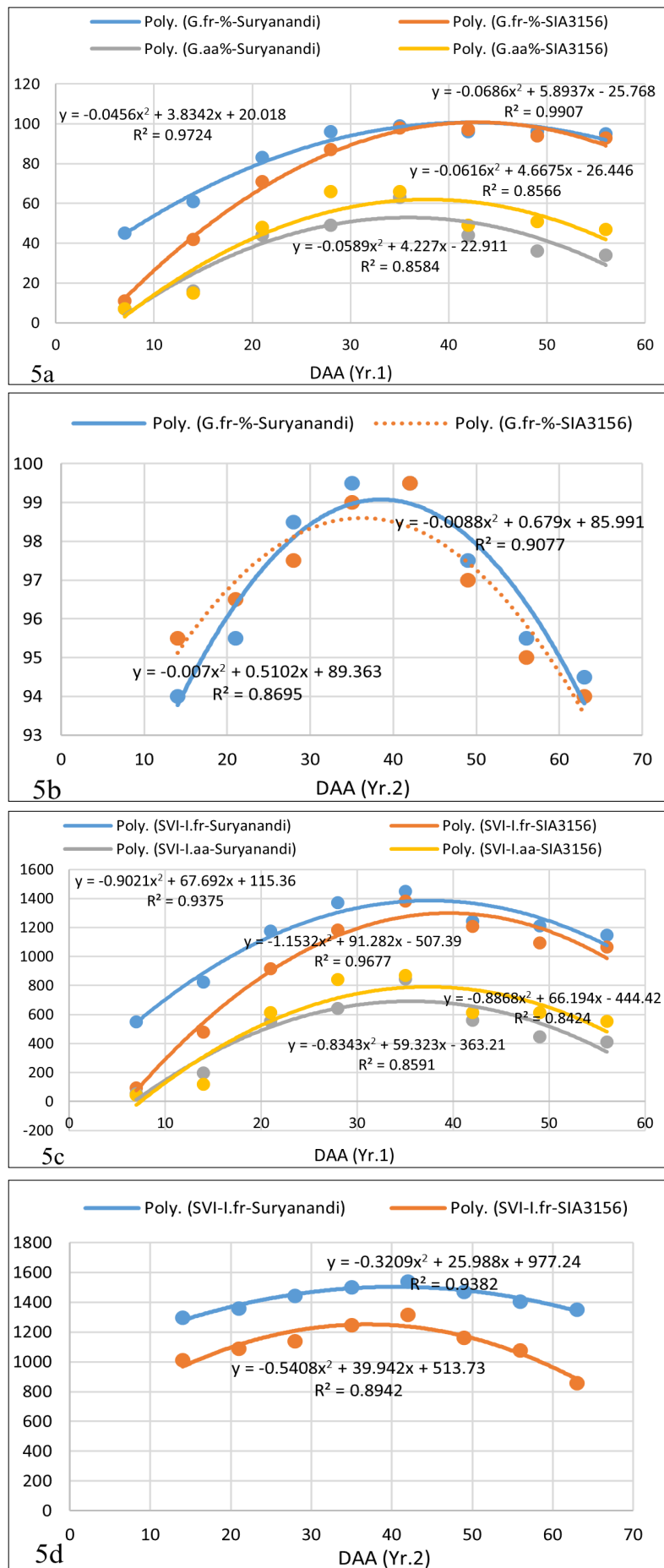


Fig. 5a-d. Polynomial regression analysis for seed germination, vigour and storability traits against days after anthesis (DAA) during year 1 (Yr.1) and year 2 (Yr.2) in foxtail millet. Dots represent individual observations in regression analysis of different traits. **a, c.** germination and seedling vigour index-I of fresh seeds (G.fr %, SVI-I.fr) and aged seeds (G.aa %, SVI-I.aa) in year 1 (Yr.1), **b, d.** germination and seedling vigour index-I of fresh seeds (G.fr %, SVI-I.fr) in year 2 (Yr.2)

in both the cultivars. Significant increase in EC values of aged seeds at later stages after 35 DAA indicates the starting of the deterioration process, with gradual loss of membrane integrity leading to reduced seed viability. The seeds harvested at 35 DAA were vigorous and more capable of reorganizing the cell membrane compared to the seeds harvested at other stages, which had lower vigour and reduced membrane integrity, as indicated by greater electrolytes leakage (Fig. 4a, b). Similarly, high vigour seeds were negatively correlated with electrolytes leakage (41). Seed quality deterioration was evident due to ageing, with increased EC and reduced enzymes activity (6, 7, 42).

α -amylase enzyme activity

During seed maturation, α -amylase is very important enzyme for the formation of storage starch granules and this enzyme is essential for the hydrolysis of stored reserves during seed germination to provide energy and nourish the developing seedling (43). The α -amylase activity was maximum in seeds harvested during year 1 at 21 DAA and later the activity remained stable until 42 DAA; however, at later stages it decreased, as observed at 5th day of germination and remained more or less same as observed on the 3rd and 10th days of seed germination (Fig. 6). During seed germination test, the α -amylase activity increased gradually until 5th day of seed germination and then started declining by the end of the test at 10 days. Seed vigour and storability are affected initially by harvesting conditions, which was reflected by the decrease in α -amylase activity (44). The α -amylase activity was high during the later stages of seed germination with the seeds harvested at full maturity and with higher vigour (6, 7, 45).

The study clearly highlighted the effects of seed maturation stages and the influence of two different post-rainy seasons on seed yield, germination, seedling vigour and storability and revealed that the seeds reached to PM at 35 DAA during year 1 and at 38 DAA during year 2 in foxtail millet cultivars. The storability was highest with the seeds harvested at 35 DAA, which had significantly higher germination, seedling growth and vigour, all of which were reduced at a faster rate during later harvest stages, as reflected by increased electrolyte leakage. The seeds harvested at PM are superior in seed quality under stress conditions (46). Immature seeds with poor quality can potentially lead to poor plant stand establishment and consequent decrease in productivity of the crop. During delayed

harvests, the seeds get exposed to adverse dry weather conditions, which can lead to seed shattering and damage seed quality (47). It is important to identify the appropriate stage of seed maturity, with minimal loss in yield and quality, as the protection mechanisms are built during the late seed maturation phase (6, 7, 30, 31, 48). Early harvesting of seeds with inadequate development of essential structures and protection mechanisms may result in poor quality (29). The variation in the levels of late embryogenesis abundant (LEA) proteins during seed maturation impacts desiccation tolerance and seed viability (49).

Seed development begins shortly after fertilization and continues until the seed reaches its maximum fresh weight and maturation and the final phase of seed development continues until harvest (50). The stages of seed development and maturation are identified by changes in seed moisture, dry matter accumulation, desiccation tolerance and the achievement of peak seed vigour and storability at harvest maturity (HM). When peak seed vigour aligns with PM, it generally indicates the optimal time for harvest (51). Thus, HM refers to the stage in seed development when the majority of the seeds are most suitable for harvesting, producing high-quality seeds with desirable traits such as storability and handling properties (10). PM marks the end of the seed filling phase, whereas HM occurs at the point when maturation drying is complete (8). The HM is the stage when majority of the seeds in the plot are ready for harvesting, ensuring both high quality and yield while considering storage, handling characteristics to prevent mechanical damage and minimizing field losses due to ineffective harvesting equipment (10). In practice, the timing of HM can vary across crops and weather conditions. The term HM is not clearly defined, as it can differ depending on the crop, farming systems and geographical locations (9).

In foxtail millet, the highest seed yield and quality were observed with the harvests at 35 DAA in year 1 and 38 DAA in year 2, thus revealing that PM generally occurs between 35 and 38 DAA and the optimal harvest window is between 35 and 42 DAA during the post-rainy season. Harvesting beyond this point of PM resulted in reduced yield from seed shattering and a decline in seed quality and storability, caused by the deterioration of seeds in the field due to adverse weather conditions during the summer months. Therefore, in foxtail millet the study clearly indicated that during post-rainy season, the PM is the correct

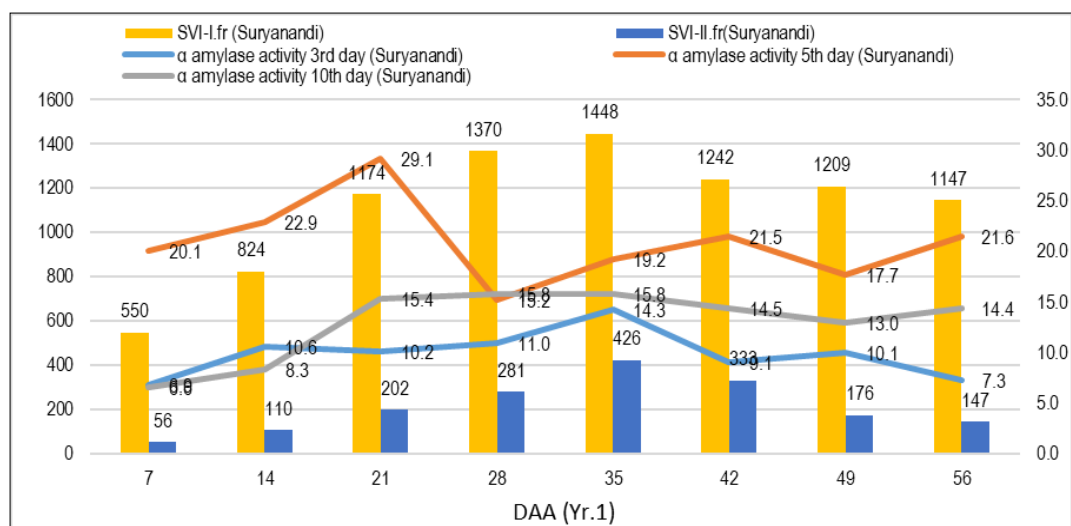


Fig. 6. Effect of different stages of seed harvests (DAA) during year 1 (Yr.1) on α -amylase activity ($\mu\text{mol maltose} \cdot \text{min}^{-1} \cdot 100 \text{ seeds}^{-1}$) at 3rd, 5th and 10th day of seed germination test period in relation with seedling vigour index of fresh seeds (SVI-I.fr and SVI-II.fr) in foxtail millet.

stage of seed harvest and hence the stage of HM coincides with PM. In foxtail millet and other small millets, the indeterminate growth habit, uneven maturity, lodging and seed shattering are some of the key problems that limit the yield. Environmental factors and agronomic practices can significantly affect the maturity stage of the seed crop (52). Predictions made using a second-order polynomial regression model for seed yield, germination, vigour and storability closely aligned with the identified stages of physiological and harvest maturity in foxtail millet cultivars. The polynomial regression model was also used to predict physiological and harvest maturity stages based on seed physiological and biochemical traits (6, 7, 24, 46, 53).

Conclusion

The study examined the impact of seed maturation on the physiological seed quality traits as well as the seed yield of foxtail millet during two post-rainy seasons. The results provided valuable insights revealing that PM generally occurs between 35 and 38 DAA and the optimal harvest window is between 35 and 42 DAA during the post-rainy season in foxtail millet. Harvesting too early or too late, depending on environmental conditions, can lead to significant losses in both seed yield and quality. The findings contribute to improved timing of harvest, helping to mitigate the adverse effects of premature or delayed harvesting and ensuring maximum seed yield, vigour and storability in foxtail millet. The visual signs identified on the panicle and seeds at the PM stage could serve as effective morphological indicators for judging the appropriate stage of harvest to ensure high-quality seed production in foxtail millet. While the current results are promising, their generalization across the foxtail millet cultivars requires validation. To ensure the broader applicability of these findings to foxtail millet cultivation, it is essential to conduct further investigations involving a greater diversity of cultivars across diverse locations and growing seasons.

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Authors' contributions

KN, HK and VR conceptualized, designed and conducted the experiments. KN and DIK analyzed the data and interpreted. KN, HK, SC and TSC prepared the manuscript. All authors read and approved the final manuscript for submission.

Compliance with ethical standards

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

Ethical issues: None

References

1. Yang X, Wan Z, Perry L, Lu H, Wang Q, Zhao C, et al. Early millet use in northern China. *Proc Natl Acad Sci USA*. 2012;109(10):3726. <https://doi.org/10.1073/pnas.1115430109>
2. Longvah T, Ananthan R, Bhaskarachary K, Venkaiah K. Indian food composition tables. Hyderabad: National Institute of Nutrition, Indian Council of Medical Research. 2017.
3. Geervani P, Eggum BO. Nutrient composition and protein quality of minor millets. *Plant Foods Hum Nutr*. 1989;39(2):201-08. <https://doi.org/10.1007/BF01091900>
4. Itagi S, Naik R, Bharati P, Sharma P. Readymade foxtail millet mix for diabetics. *Int J Sci Nat*. 2012;3(1):47-50.
5. Diao X. Production and genetic improvement of minor cereals in China. *Crop J*. 2017;5(2):103-14. <https://doi.org/10.1016/j.cj.2016.06.004>
6. Kannababu N, Deepika C, Venkateswarlu R, Hariprasanna K, Das IK. Physiological maturity of seeds in kodo millet (*Paspalum scrobiculatum* L.) cultivars across seasons. *Plant Physiol Rep*. 2023;28(2):209-20. <https://doi.org/10.1007/s40502-023-00725-9>
7. Kannababu N, Amasiddha B, Venkateswarlu R, Das IK, Prabhakar B, Tonapi VA. Determination of physiological and harvestable mass-maturity of seeds during rainy and post-rainy seasons in barnyard millet (*Echinochloa frumentacea* (Roxb). Link). *Range Manag Agrofor*. 2023;44(1):84-94.
8. Harrington JF, Kozlowski TT. Seed storage and longevity. *Seed Biol*. 1972;3:145-245. <https://doi.org/10.59515/rma.2023.v44.i1.10>
9. Ellis RH. Temporal patterns of seed quality development, decline and timing of maximum quality during seed development and maturation. *Seed Sci Res*. 2019;29(2):135-42. <https://doi.org/10.1017/S0960258519000102>
10. Bewley JD, Black M, Halmer P. The encyclopedia of seeds: science, technology and uses. Wallingford: CABI. 2006.
11. Finch-Savage WE, Bassel GW. Seed vigour and crop establishment: extending performance beyond adaptation. *J Exp Bot*. 2016;67(3):567-91. <https://doi.org/10.1093/jxb/erv490>
12. Eskandari H. Seed quality changes in cowpea (*Vigna sinensis*) during seed development and maturation. *Seed Sci Technol*. 2012;40(1):108-12. <https://doi.org/10.15258/sst.2012.40.1.12>
13. Ghassemi-Golezani K, Hosseinzadeh-Mahootchy A. Changes in seed vigour of faba bean (*Vicia faba* L.) cultivars during development and maturity. *Seed Sci Technol*. 2009;37(3):713-20. <https://doi.org/10.15258/sst.2012.40.1.12>
14. Samarah NH, Abu-Yahya A. Effect of maturity stages of winter-and spring-sown chickpea (*Cicer arietinum* L.) on germination and vigour of the harvested seeds. *Seed Sci Technol*. 2008;36(1):177-90. <https://doi.org/10.15258/sst.2008.36.1.19>
15. Vidigal DD, Dias DC, Dias LA, Finger FL. Changes in seed quality during fruit maturation of sweet pepper. *Sci Agric*. 2011;68:535-39. <https://doi.org/10.1590/S0103-90162011000500004>
16. Ramya M, Yogeesh HS, Bhanuprakash K, Gowda RV. Physiological and biochemical changes during seed development and maturation in onion (*Allium cepa* L.). *Vegetable Sci*. 2012;39(02):157-60.
17. Oliveira GE, Pinho RG, Andrade TD, Pinho ÉV, Santos CD, Veiga AD. Physiological quality and amylase enzyme expression in maize seeds. *Cienc Agrotec*. 2013;37:40-48. <https://doi.org/10.1590/S1413-70542013000100005>
18. International Seed Testing Association (ISTA). International rules for seed testing. Bassersdorf: ISTA. 2015.
19. Delouche JC, Baskin CC. Accelerated aging techniques for predicting the relative storability of seed lots. *Seed Sci Technol*. 1973;1:427-52.

20. Bernfeld P, Colowick S P, Kaplan N O. Methods in Enzymology. Academic Press. 1955:145-158.
21. Leprince O, Pellizzaro A, Berriri S, Buitink J. Late seed maturation: drying without dying. J Exp Bot. 2017;68(4):827-41. <https://doi.org/10.1093/jxb/erw363>
22. Marcos-Filho J. Fisiologia de sementes de plantas cultivadas. 2. ed. Londrina: ABRATES. 2015;659.
23. Araujo EF, Araujo RF, Sofiatti V, Silva RF. Maturation of sweet-corn seeds: Super Sweet group. Rev Bras Sementes. 2006;28:69-76. <https://doi.org/10.1590/S0101-31222006000200009>
24. Shaheb MR, Islam MN, Nessa A, Hossain MA. Effect of harvest times on the yield and seed quality of French bean. SAARC J Agric. 2015;13(1):1-3. <https://doi.org/10.3329/sja.v13i1.24175>
25. Ma ChunHui MC, Cheng Jun CJ, Han JianGuo HJ, Chen JianXin CJ, Yang ZhongLiang YZ, Dong YuMin DY. Study on the dynamic changes of physiology and biochemistry during the seed development of tall fescue in Xinjiang. Pratacult Sci. 2002;11(4):76-80.
26. Ellis RH, Pieta Filho C. The development of seed quality in spring and winter cultivars of barley and wheat. Seed Sci Res. 1992;2(1):9-15. <https://doi.org/10.1017/S0960258500001057>
27. Maiti RK, Raju PS, Biding FR. Studies on germinability and some aspects of pre-harvest physiology of sorghum grain. Seed sci technol. 1985;13(1):27-35.
28. Tonapi VA, Varnavasiappan S, Navi SS, Ravinder Reddy C, Karivatharaju TV. Effect of environmental factors during seed development and maturation on seed quality in *Sorghum bicolor* (L.) Moench. Plant Arch. 2006;6(2):515-19.
29. Ekpong B, Sukprakarn S. Seed physiological maturity in dill (*Anethum graveolens* L.). Agric Nat Resour. 2008;42(5):1-6.
30. Jalink H, Frandas A, Schoor RV, Bino JB. Chlorophyll fluorescence of the testa of *Brassica oleracea* seeds as an indicator of seed maturity and seed quality. Sci Agric. 1998;55:88-93. <https://doi.org/10.1590/S0103-90161998000500016>
31. Demir I, Ashirov AM, Mavi K. Effect of seed production environment and time of harvest on tomato (*Lycopersicon esculentum*) seedling growth. 2008;1:1-10. <https://doi.org/10.3923/rjss.2008.1.10>
32. Parthasarathi T, Velu G, Jeyakumar P. Impact of crop heat units on growth and developmental physiology of future crop production: A review. Res Rev J Crop Sci Technol. 2013;2(1):1-1.
33. Tzudir L, Bera P S, Chakraborty P K. Impact of temperature on the reproductive development in mungbean (*Vigna radiata*). Int J Bio-Resour Stress Manag. 2015;5:194-99. <https://doi.org/10.5958/0976-4038.2014.00555.7>
34. Basave Gowda BG, Gowda SJ. Effect of stage of harvest on seed germination during storage in hybrid sorghum. Seed Res. 1999;18(3):368-69.
35. Woodward FI. The impact of low temperatures in controlling the geographical distribution of plants. Philos Trans R Soc Lond B Biol Sci. 1990;326(1237):585-93. <https://doi.org/10.1098/rstb.1990.0033>
36. Pigott CD, Huntley JP. Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range III. Nature and causes of seed sterility. New Phytol. 1981;87(4):817-39. <https://doi.org/10.1111/j.1469-8137.1981.tb01716.x>
37. Rahman SM, Ellis RH. Seed quality in rice is most sensitive to drought and high temperature in early seed development. Seed Sci Res. 2019;29(4):238-49. <https://doi.org/10.1111/j.1469-8137.1981.tb01716.x>
38. Jumrani K, Bhatia VS. Combined effect of high temperature and water-deficit stress imposed at vegetative and reproductive stages on seed quality in soybean. Indian J Plant Physiol. 2018;23(2):227-44. <https://doi.org/10.1007/s40502-018-0365-9>
39. Delouche J C. Seed production manual. National Seeds Corporation Ltd and Rockefeller Foundation. 1973.
40. ISTA. Handbook of Vigour Test Methods (3rd ed.). International Seed Testing association. 1995.
41. Fatonah K, Suliansyah I, Rozen N. Electrical conductivity for seed vigour test in sorghum (*Sorghum bicolor*). Cell Biol Dev. 2017;1(1):6-12. <https://doi.org/10.13057/cellbioldev/v010102>
42. Das R, Biswas S. Changes in biochemical and enzymatic activities with ageing in seeds of different sizes of sunflower (*Helianthus annuus* L.) under invigoration treatments. Plant Physiol Rep. 2022;27(1):81-95. <https://doi.org/10.1007/s40502-021-00610-3>
43. Damaris RN, Lin Z, Yang P, He D. The rice alpha-amylase, conserved regulator of seed maturation and germination. Int J Mol Sci. 2019;20(2):450. <https://doi.org/10.3390/ijms20020450>
44. Pollock BM, Roos EE. Seed and seedling vigour. Seed Biol I Importance Dev Germination. 1972:314-87.
45. Shephard HL, Naylor RE, Stuchbury T. The influence of seed maturity at harvest and drying method on the embryo, α -amylase activity and seed vigour in sorghum (*Sorghum bicolor* (L.) Moench). Seed Sci Technol. 1995:245-249.
46. Maria ILS, Eduardo LV, Leilson CG, Elizângela EC, Cristiane ECM, Salvador BT. Determination of harvest maturity in *Capsicum baccatum* L. seeds using physiological and biochemical markers. Aust J Crop Sci. 2015;9(11):1010-15.
47. Elias SG, Copeland LO. Physiological and harvest maturity of canola in relation to seed quality. Agron J. 2001;93(5):1054-58. <https://doi.org/10.2134/agronj2001.9351054x>
48. Jalink H, Van der Schoor R, Birnbaum YE, Bino RJ. Seed chlorophyll content as an indicator for seed maturity and seed quality. Acta Hort. 1999;15:219-28. <https://doi.org/10.17660/ActaHortic.1999.504.23>
49. Smolikova G, Leonova T, Vashurina N, Frolov A, Medvedev S. Desiccation tolerance as the basis of long-term seed viability. Int J Mol Sci. 2020;22(1):101. <https://doi.org/10.3390/ijms22010101>
50. Abdul-Baki AA, Baker JE. Are changes in cellular organelles or membranes related to vigour loss in seeds. Seed Sci Technol. 1973;1(1):89-125.
51. Patrick JW, Offler CE. Compartmentation of transport and transfer events in developing seeds. J Exp Bot. 2001;52(356):551-64. <https://doi.org/10.1093/jexbot/52.356.551>
52. Saibabu KGRS, Hussaini SH, Reddy BMM, Reddy PR. Effect of nitrogen fertilization on maturity, seed yield and quality in rice. Seed Res. 1984;12(2):51-55.
53. Lessa BF, Dutra AS, Silva TM, Santos CC, Sousa WD. Physiological maturation in seeds of sweet sorghum for foliar fertilisation with silicate. Rev Caatinga. 2017;30(3):718-29. <https://doi.org/10.1590/1983-21252017v30n320rc>

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