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RSEARCH ARTICLE

Accelerated aging test reveals quantitative nature of inheritance of seed viability in soybean [*Glycine max* (L.) Merr.]

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Abstract

Soybean [*Glycine max* (L.) Merr.], a source of premium quality protein and oil, suffers from loss of viability of the seeds during ambient storage. The current study aimed to understand the genetics of seed viability in soybean and its association with other traits through accelerated aging (AA) test. A set of 119 $F_{2:3}$ seeds were derived from the hybridization of EC1023 (highly viable; 91.87% after one year of storage) and VLS61 (poorly viable; 60.87% germination after one year of ambient storage) were tested for viability and vigor through AA test at 41± 1°C for 72 hours under~100% relative humidity. The tested seeds differed significantly for seed viability 4.16 to 71.42% and vigor index I (6.6 -1049.66) and II (13.07-1694.88). The continuous distribution of the germination of the $F_{2:3}$ seeds indicated polygenes' involvement in controlling the seeds' viability. The percent seed germination found to be positively and significantly correlated with the average seedling length (SL) (r=0.78) and seedling dry weigh (SDW) (r=0.83); Similarly, SL was found to be associated with SDW (r=0.92). The information on the inheritance of seed viability along with the vigor indices, would facilitate genetic improvement of seed viability in soybean.

Keywords: Accelerated aging test, correlation, seed viability, polygenic inheritance, vigor indices.

Introduction

Soybean [*Glycine max* (L.) Merrill] is the world's *numerouno* oilseed crop, accounting for nearly 57% of the global oilseed production. It is also the richest (40–45%) and cheapest source of plant-based protein, which contains nearly all the amino acids required by the human body for its general growth and development. Soybean also contains 18–22% oil rich in poly- and mono-unsaturated fatty acids, making it healthier for consumers. Besides oil and protein, soybean contains carbohydrates, ash, antioxidants, and several other important nutritional elements, making it an important food for our health. The soybean's de-oiled cake (DOC) has been the choice of animal growers as nutritious feed for animals, fowl, and fish. Therefore, soybean is gaining boundless popularity worldwide in the food, health, pharmaceutical and cosmetic industries.

In terms of area and production of soybean, India ranks 5th globally; however, the productivity is very low, which is hovering around 10 q/ha as against about 25 q/ha world average. Amongst several other factors, the non-availability of quality seeds during the sowing period is an important factor affecting soybean production and productivity in the country. Rapid loss of viability of the seeds during ambient storage decreases the quality of the seeds. Loss of seed viability is often hastened by the genotypic, climatic and storage conditions and it is severe in warm and humid climates (Dargahi et al. 2014). India being a sub-tropical

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country, the problem of seed viability loss is critical here. From harvest to next planting, seed viability in most of the Indian soybean varieties goes down to around 70% under ambient storage conditions (Singh and Ram 1986). Bhattacharya and Raha (2002) reported a decrease of the germination of soybean seeds to zero under 9 months of ambient storage. Poor viability of the seeds demands enhancing the seed rate for maintaining the plant stand in the field, which increases the cost of production and diminishes the farmer's income. It is, therefore important to understand the real cause of viability loss in the seeds so that effective measures can be taken to keep them viable for a longer period.

Seed viability refers to the competence of an embryo to remain alive inside a seed and to show normal germination and growth when sown in the field. Lots of factors influence the viability of soybean seeds, viz., physical (seed coat, seed color, seed size, seed coat permeability, gap between seed coat and cotyledons), biochemical (amount of hydroxylated fatty acids, accumulation of ROS and antioxidants), physiological (electrolyte leaching during imbibition, environmental (temperature, humidity, water stress), and genetics (genes and QTLs) (Sooganna et al. 2016). For enhancing the viability of soybean seeds through the breeding approach, it is essential to understand the trait's genetic control, i.e., whether seed viability is controlled by single or polygenes. However, findings about genetic control of seed viability in soybean are hugely diverse and contradictory. Kueneman (1983) reported the influence of maternal factors while Dao et al. (1999) observed monogenic and di-genic control on seed longevity in ambient storage. Adsul et al. (2018) also observed monogenic control of seed longevity in soybean. Clerkx et al. (2004) considered seed storability as a complex trait controlled by several genes coupled with environmental conditions during seed formation, harvest, and storage. The advent of molecular markers helped in the identification and mapping of several quantitative trait loci (QTL) for seed viability in soybean; however, the number of QTLs reported varied considerably, such as two (*Ha1* and *Ha2*) (Kumar et al. 2019, Zhang et al. 2008), three (Dargahi et al. 2014) and five (*VIS 1-5*) (Watanabe et al. 2004). Association of SSR markers *viz*., Satt434, Satt538, Satt281 and Satt598 (Singh et al. 2008), and Satt371, Satt453 and Satt618 (Hosamani et al. 2013) with seed storability have been reported. Sooganna et al. (2016) reported that SSR marker Satt423 could distinctly differentiate good storing soybean genotypes from poor ones. Permeable seeds are relatively less viable than impermeable ones. Sun et al. (2015) identified a base substitution (T→G) in a gene (*GmHs1-1)* associated with calcium content in the seed coat that transformed the impermeable seed coat to permeable ones. Jang et al. (2015) made a similar observation. Going by these findings, the report of genetic control of seed viability appears to be diverse and inconsistent. Moreover, phenotyping the seeds for seed viability trait is critical for understanding the genetic control of the trait. Usually, viability is expressed in terms of germination after keeping the seeds under ambient storage conditions. However, it is a time-consuming process influenced by several factors, including storage conditions. Accelerated aging (AA) has been used as an alternative to the conventional storage method of aging. Besides AA testing, several other methods *viz.* Electrical conductivity, cold test, sodium hypochlorite etc. are also available for the determination of age of seeds. However, AA test is rapid, and precise and the results are comparable to the test under conventional storage (Egli et al. 1978; Hosamani et al. 2013; Sooganna et al. 2016; Tekrony et al. 1980). Therefore, this study attempted to understand the genetic control of seed viability in soybean using an intra-specific segregating population through AA testing.

Materials and methods

Plant material

The experimental material consisted of 119 $F_{2:3}$ plants developed from an intra-specific cross between soybean genotypes EC1023 (yellow seeded with good seed storability i.e., 91.87% germination after 1 year of ambient storage) and VLS61 (yellow seeded with poor storability i.e., 60.87% germination after 1 year of ambient storage). Genotypic analysis was done in 119 $F_{2:3}$ plants, whereas, due to some uncontrolled disease incidence as well as loss of germination during the accelerated aging test, phenotypic data from 51 plants were recorded (Table 1). Parental genotypes were obtained from the Soybean Laboratory, Division of Genetics, ICAR-IARI New Delhi.

Standardization of accelerated aging (AA) parameters

For the standardization of the accelerated aging vigor test in soybean, seeds of DS9712 a popular and commonly grown soybean variety of North India, were taken and subjected to two different temperatures viz., 41 and 43°C for three different time duration *i.e.,* 48, 72 and 96 hours under ~100% relative humidity (Table 2). The artificially aged seeds were subjected to a standard germination test and data on germination percent and other viability-related parameters were recorded on the 8th day of germination.

Accelerated aging vigor test

After the temperature and time duration standardization for the AA vigor test (Table 2 and Fig. 1), the viability of the parental genotypes and $F_{2:3}$ populations were examined. Initially, the chamber of the seed germinator was sterilized with alcohol to avoid the fungal contamination of the seeds. The tested seeds were then packed in net cloth bags stapled with a stapler pin and placed in the seed germination

chamber (Fig 2). The Age of the seeds (parental and $F_{2:3}$ seeds) was increased artificially by exposing it to high temperature (41°C±1) and relative humidity (~100%) for 72 hours, followed by a germination test as per ISTA, 2009. Seed germination percent, seedling length, dry seedling weight, vigor index I and II were calculated. As per vigor test protocol, data on germination (%), seedling length, seedling dry weight, vigor index I and II were recorded from the seeds that produced normal seedlings only i.e., seedlings with normal root and shoot growth, having shoot: root ratio nearly unity, healthy and free from seed-borne diseases and pests. Seedlings with abnormal growth (showing high root to shoot ratio, high shoot to root ratio, less root hair development, decayed or deformed radicle of germination seed etc. and infected by pest and diseases) were discarded.

Seed germination test

The germination of the seeds was tested as per ISTA protocol. The test was conducted in two replications of 100 seeds each following the 'between paper method'. The seeds were incubated in the seed germination cabin maintained at a temperature of 25 ± 1 0°C and RH ~95%. Germination data were recorded on the 5th and 8th days after sowing. The number of germinated seeds with normal seedlings was only counted and the percentage of germination was obtained. The viability of the seeds was expressed in terms of seed germination (%) i.e., the higher the seed germination (%), the higher is the seed viability of the plant/genotype.

Vigor indices

Seed vigor is the summation of all properties that determine the overall activity and performance of the seed lots having significant germination in a variable environment (ISTA). Seed lot showing higher seed vigor indices are regarded to be more vigorous (Abdul-Baki and Anderson 1973). The dry weight of $F_{2:3}$ seedlings was taken after 16 hours of oven drying. The formula for vigor index I and II were as follows:

Vigor Index I = Standard germination (%) × Average seedling length (cm) (Maisuria and Patel 2009); Vigor Index II = Standard germination (%) × Average seedling dry weight (mg or g) (Dezfuli et al. 2008).

Results

Standardization of accelerated aging (AA) test

During the standardization of the parameters for the AA test, it was found that the germination of the seeds treated with 41°C for 48hrs was 22% with very high vigor index I (320.76) and II (3007.40). It indicated failure of the temperature and duration of the treatment in significantly impacting the seed's aging. Similarly, germination of the seeds treated at 41°C for 72 hours was 14% with moderate vigor index I (163.24) and II (1691.48). The seeds subjected to 41°C for 96 hours had 12% germination and low vigor index I (126.54) and II (660.00). With the increase in temperature and duration, the aging caused to the seeds also increased (Table 2 and Fig 1). Correspondingly, seed viability, vigor, and percentages of normal seedlings were decreased. It was observed that lower temperature and shorter duration was not sufficient to cause an aging effect on the seeds, while higher temperature and longer duration was too much damaging to the seed. By evaluating the seed germination (%) and vigor index I and II, temperature 41^{0}C and duration, 72 hrs under ~100% RH was chosen for the accelerated aging test of the tested seeds.

Inheritance of seed viability in soybean

After accelerated aging, the germination of EC1023 (high viable genotype) and VLS61 (poor viable genotype) was 40% and 14%, respectively, which clearly indicated the significant differences in the viability between the two parental lines. The germination of the $F_{2:3}$ seeds ranged from 4.16% to 71.42% with a mean of 17.31% (Table 3). The range of seed germination in the $F_{2:3}$ seeds surpassed the range of germination of the parental genotypes i.e., 14 to 40%, and it showed a continuous distribution from low to high (Fig. 3). The continuous distribution of the data indicated the involvement of more than one gene in controlling the seed viability trait in soybean. The presence of a greater number of phenotypic classes and appearance of the transgressive segregants in the segregating generation also confirms

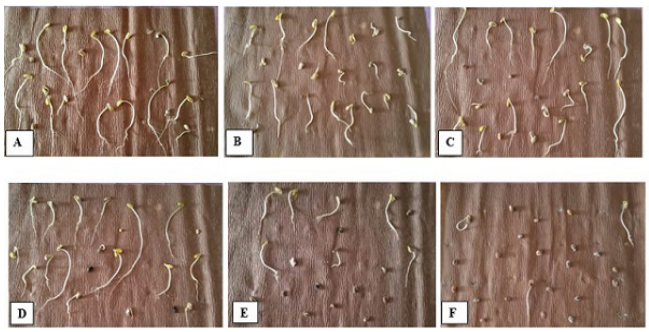

Fig. 1. Standardization of AA vigor test in soybean. Treatment of seeds with A: 41°C for 48 h and G was 22%, B: 41°C for 72 h and G was 14%, C: 41°C for 96 h and G was 12%, D: 43°C for 48 h and G was 10%, E: 43°C for 72 h and G was 8% and, F: 43°C for 96 h and G was 0%.

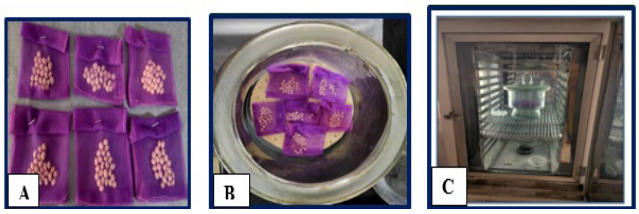

Fig. 2. Accelerated aging vigor test (A) Preparation of seed bags, (B) Seed bags kept in desiccators and (C) Desiccator containing seed bags along with thermometer kept inside the seed incubator or germinator.

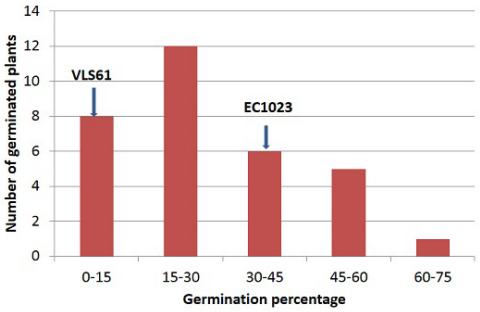

Fig. 3. Frequency distribution of germination percentage of the seeds in $F_{2:3}$ generation.

the involvement of a large number of genes and their recombination in the expression of the phenotypes.

Vigor indices and character association

In the AA test, vigor of the seeds was measured in two indices, viz., vigor index I and II. The vigor index is the product of the germination percentage and average seedling length (cm) of normal seedlings (Maisuria and Patel 2009). Similarly, the vigor index II is the product of germination percentage and average seedling dry weight (mg) (Dezfuli et al. 2008). In this test, the vigor index I ranged from 6.6 to 1049.66, and the vigor index II ranged from 13.07 to 1694.88 (Table 3), which indicated inherent variation among the seeds in its field performance potentialities. As per norms, the seedlings having both indices high would perform better in the field than others. In this test, plant no. C13-P11 was found to have both the vigor indices high i.e. 1049.66 and 1452.49, respectively (Table 1 and Fig. 4), and predicted to perform well in viability during storage. Contrarily, plant no. C10-P7 was found to have both the vigor indices low i.e., 32.03 and 13.31, respectively, and predicted to perform poorly during storage.

Character association

In this experiment, the correlation of seed viability measured through germination percentage was studied with seedling length and dry seedling weight. It was found that germination was positively and significantly associated with average seedling length (r=0.78) and dry seedling weight (r=0.83) (Table 4). Similarly, seedling length was found to be positively and significantly associated with dry seedling weight (r=0.92). It indicated that seed viability is associated with several other traits; hence, selection for this trait would be relatively easy.

Discussion

One of the principal constraints in soybean cultivation is the sustention of seed viability until subsequent planting, as the viability of the seeds begins declining after physiological maturity (Crookston and Hill 1978) followed by fast decline during ambient storage (Surki et al. 2012). Loss of viability is

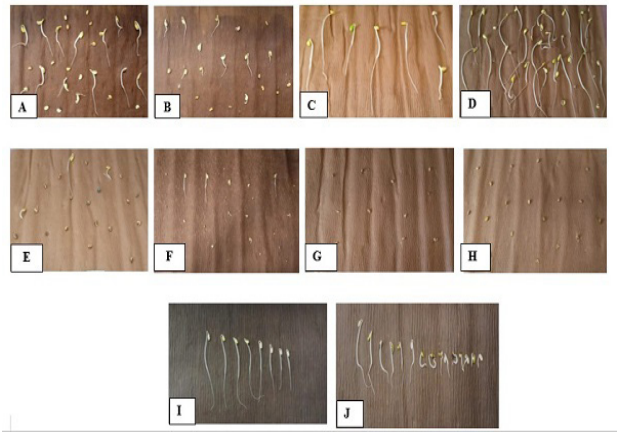

Fig. 4. Variation in the germination percentages after AA test in parental genotypes and $F_{2:3}$ populations. A: Germination in EC1023, B: Germination in VLS61, C and D: Seedling of highly viable seeds, E and F: Seedlings of poor-viability, G and H: Non-germinated seeds, I: High vigor seedling and, J: Seeding with diverse vigor level.

more acute in tropical and sub-tropical regions (Hang et al. 2015), including India. Poor longevity of the soybean seeds affects seedling vigor. Crop stands in the field and, ultimately the seed yield (Zhang et al. 2019). Therefore, improving seed viability in soybean is important to increase overall crop production (Dargahi et al. 2014). Studies attempting to figure out the component(s) responsible for viability loss hinted that numerous genetic and non-genetic factors such as moisture content, relative humidity, oxygen pressure, the temperature of storage etc., influence directly or indirectly inflicting the seeds to lose viability (Groot et al. 2012, Potts et al. 1978). Seed size, seed composition, seed coat integrity, mechanical damage, field weathering, etc. deteriorates the seed quality leading to delayed seed germination, abnormal plant growth and poor plant stand in the field thereby reducing crop yield (Ghassemi-Golezani et al. 2010). The factors causing loss of viability became more damaging with the increased period of ambient storage; however, response to it varied with genotype, species and other varietal characters (Kurdikeri et al. 2000). The wild species of soybean are the excellent reservoirs of longevity-related genes, maintain viability for a longer period of time (Chandra et al. 2022) and need to be used in the breeding programs to introgress this trait into cultivated soybean (Kumar et al. 2019, Talukdar and Shivakumar 2016, Zhou et al. 2010). Thus, understanding the genetic basis and its deployment could offer a long-lasting solution to the problem of rapid viability loss in soybean. In the present study, the $F_{2:3}$ seeds of the cross EC1023 x VLS61 were subjected to accelerated aging followed by germination test. The germination in the seeds ranged from 4.16 to 71.42%, indicating variability in the seeds for viability. The range of seed germination in the $F_{2:3}$ seeds (4.16-71.42%) went beyond the range of germination of parental genotypes i.e., 14-40%, which indicated the appearance of transgressive segregants. The germination

Table 1. List of various parameters recorded from the progenies of F_2 plants

S. No.	F_2 Plant No.	Germination %	Seedling length (cm)	Seedling dry weight (mg)	Vigor Index I	Vigor Index II
1	C6 P-3	16.66	9.74	11.66	162.27	194.25
2	C6 P-5	0.00	0.00	0.00	0.00	0.00
3	C6 P-6	0.00	0.00	0.00	0.00	0.00
4	C6 P-7	4.34	11.90	8.40	51.64	36.45
5	C6 P-8	14.28	9.60	3.20	137.08	45.69
6	C6 P-9	07.69	7.70	1.70	59.21	13.07
7	C6 P-19	17.33	12.65	21.36	219.22	370.16
8	C6 P-21	0.00	0.00	0.00	0.00	0.00
9	C13 P-1	0.00	0.00	0.00	0.00	0.00
10	C13 P-2	0.00	0.00	0.00	0.00	0.00
11	C13 P-3	5.00	7.10	7.60	35.50	38.00
12	C13 P-4	0.00	0.00	0.00	0.00	0.00
13	C13 P-7	11.36	11.92	15.12	135.41	171.76
14	C13 P-8	0.00	0.00	0.00	0.00	0.00
15	C13 P-10	0.00	0.00	0.00	0.00	0.00
16	C13 P-11	57.14	18.37	25.42	1049.61	1452.50
17	C13 P-12	71.42	12.49	15.95	892.03	1139.15
18	C13 P-13	45.00	18.55	30.96	834.75	1393.20
19	C13 P-41	44.44	16.53	25.72	734.59	1143.00
20	C13 P-42	55.55	17.88	30.36	993.23	1686.50
21	C13 P-43	28.57	17.15	19.87	489.97	567.68
22	C10 P-1	10.71	14.26	15.00	152.72	160.65
23	C10 P-2	18.18	11.59	12.75	210.70	231.79
24	C10 P-3	0.00	0.00	0.00	0.00	0.00
25	C10 P-4	0.00	0.00	0.00	0.00	0.00
26	C10 P-5	0.00	0.00	0.00	0.00	0.00
27	C10 P-6	0.00	0.00	0.00	0.00	0.00
28	C10 P-7	4.16	7.70	3.20	32.03	13.31
29	C10 P-8	27.50	9.72	10.56	267.30	290.40
30	C10 P-9	15.38	10.00	7.00	153.80	107.66
31	C10 P-10	5.26	9.30	7.85	48.91	41.29
32	C10 P-11	41.66	17.23	20.92	717.80	871.52
33	C10 P-12	18.18	22.40	29.35	407.23	533.58
34	C10 P-13	14.28	11.00	15.15	157.08	216.34
35	C10 P-14	0.00	0.00	0.00	0.00	0.00
36	C10 P-15	40.00	18.57	28.00	742.80	1120.00
37	C10 P-16	0.00	0.00	0.00	0.00	0.00
38	C10 P-20	33.33	14.84	20.26	494.61	675.26
39	C10 P-21	15.00	17.40	17.46	261.00	261.90
40	C10 P-22	17.64	12.10	16.80	213.44	296.35
41	C10 P-24	37.83	14.37	19.32	543.61	730.87
42	C10 P-25	25.00	11.13	5.46	278.25	136.50
43	C10 P-26	47.82	15.89	20.49	759.85	979.83
44	C10 P-27	0.00	0.00	0.00	0.00	0.00

45	C10 P-28	20.00	11.38	18.12	227.60	362.40
46	C10 P-35	53.84	17.17	31.48	924.43	1694.88
47	C10 P-36	0.00	0.00	0.00	0.00	0.00
48	C10 P-37	0.00	0.00	0.00	0.00	0.00
49	C10 P-42	23.33	18.65	19.08	435.10	445.13
50	EC1023	40.00	9.10	33.06	364.00	1322.40
51	VL5-61	14.00	5.58	8.20	78.12	114.80

Table 2. Standardization of accelerated aging vigor test in soybean

Temperature and Time duration	First Count (No.)	Number of Normal seedlings	Number of Abnormal seedlings	Number of Fresh and germinated seeds	Number of Dead seeds	Germination %	Seedlings length (cm)	Seedlings dry weight (mg)	Vigor Index I	Vigor Index II
41°C, 48hrs	42.00	11.00	27.00	7.00	5.00	22.00	14.58	136.70	320.76	3007.40
41°C, 72hrs	40.00	7.00	19.00	5.00	9.00	14.00	11.66	120.85	163.24	1691.48
41°C, 96hrs	35.00	6.00	21.00	9.00	13.00	12.00	10.52	55.00	126.54	660.00
43°C, 48hrs	30.00	5.00	25.00	8.00	12.00	10.00	9.62	76.80	96.20	768.00
43°C, 72hrs	24.00	4.00	14.00	11.00	21.00	8.00	8.32	35.20	66.56	281.60
43°C, 96hrs	14.00	0.00	10.00	8.00	32.00	0.00	0.00	0.00	0.00	0.00

Table 3. Range and mean of various parameters in $F_{2:3}$ populations

S. no.	Character	Range	Mean
1	Germination (%)	4.16-71.42	17.31
2	Seedling Length (cm)	7.1-22.4	17.45
3	Seedling dry weight (mg)	1.7-31.48	10.76
4	Vigor index I	6.6-1049.66	261.69
5	Vigor index II	13.07-1694.88	355.53

Table 4. Correlation between different parameter in $F_{2:3}$ populations

	Germination %	Seedling Length	Seedling Dry Weight
Germination %	1		
Seedling Length	0.783*	1	
Seedling Dry Weight	0.832*	0.917 *	1

* Indicates significance at 0.01

data while plotted in a bar diagram showed continuous distribution keeping the parental data within the range. It thus indicated the involvement of polygenes or quantitative trait loci (QTL) in controlling the seed viability trait in soybean. Clerkx et al. (2004) indicated the seed viability to be a complex trait controlled by several genes and also affected by environmental conditions during seed formation, harvest and storage. Hosamani et al. (2013) indicated the genetic makeup of soybean genotypes to determine the viability of the seeds during storage. The numbers of QTL reported for seed viability traits were found to vary considerably from two (*Ha1* and *Ha2*) (Kumar et al. 2019; Zhang et al. 2008), three (Dargahi et al. 2014) to five (*VIS 1-5*) (Watanabe et al. 2004). Verma and Ram (1987) reported the involvement of 2 to 4 genes for seed longevity in soybean. In this study, variation in germination percentage and appearance of the transgressive segregants in the segregating generation confirmed the involvement of a large number of genes in controlling viability in soybean seeds.

Testing the viability of seeds through ambient storage is a time taking process. Contrarily accelerated aging mimicking the ambient storage is a rapid and effective approach to viability testing in soybean seeds. Nowadays, the AA test is one of the most lucrative tests for seed vigor. Artificial exposure of the seeds to higher temperature and humidity for a prescribed time period provides the simulation results with natural aging (Egli et al. 1978; TeKrony et al. 1980). In this study, the temperature and duration of treatment were optimized for accelerated aging, and 41±1°C and nearly 100% RH for 72 hours were used for the treatment. This condition matched with that reported earlier (Dargahi et al. 2014, ISTA 2009). Highly vigorous seed lots are more tolerant to stressful conditions and produce higher percentages of normal seedlings (Rastegar et al. 2011). The aging treatment

remarkably influences the germination characteristics such as germination percentage, germination uniformity, and germination indices (Rastegar et al. 2011, Ruzrokh et al. 2003, Verma 1 et al. 2003) which leads to the reductions in seed quality and performance (Mc Donald 1999). Unlike germination data, the vigor indices reflect the true potential of seed during germination and field emergence (TeKrony et al. 1989), the higher the vigor indices better is the field performance and stand establishment (Finch and Bassel 2016). In this study, we tried to measure the seed viability in term of their seed vigor index I and II, which ranged from 6.6 -1049.66 and 13.07 - 1694.88, respectively. The seedlings having both the indices high would perform better in the field than others. Accordingly, plant no. C13-P11 with high vigor indices (1049.66 and 1452.49) is expected to perform better in the field. The effectiveness of accelerated aging in testing viability was proved in several other crops, including mungbean (Bishnoi and Santose 1996) and chickpea (Dahiya et al. 1997). Accelerated aging in cowpea was found to affect all physiological parameters such as germination percentage and vigor index (Kapoor et al. 2010). The decrease in germination percent and other indices can be related to physiological and biochemical changes during seed aging (Ghassemi-Golezani et al. 2010). Thus, the vigor index offers the possibility of categorizing seed lots into classes of seed quality.

In this study, an artificial aging test in the seeds of an $F_{2:3}$ generation indicated that polygenes control viability of the seeds. Further, a significant and positive association of the viability trait with seedling length and dry seedling weight was also established. The findings of this study would pave the way for mapping of the QTL for seed viability and genetic improvement of seed viability in soybean through molecular breeding.

Authors' contribution

Conceptualization of research (AT, MS); Designing of the experiments (AT, MS); Contribution of experimental materials (AT, SKL); Execution of lab experiments and data collection (MS, RRY, AK, NKKR, SS, MY, RK, MT); Analysis of data and interpretation (MS, RRY, SC, SB, AR); Preparation of the manuscript (MS, AT).

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