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Genetic variability for Seed Viability, Seedling Vigor and Cytotoxic Compound Accumulation in Groundnut (*Arachis hypogaea* L.) upon Accelerated Ageing

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A B S T R A C T

Groundnut being one of the important oilseed crops rapidly deteriorates during storage due to accumulation of cytotoxic compounds leading to loss of viability and seedling vigor. Although seeds deteriorate naturally during storage, the time taken for complete deterioration process is longer. Globally, researchers employed accelerated ageing method efficiently to screen large number of genotypes to assess the genetic variability for cellular tolerance. In our study, accelerated ageing technique was standardized by exposing the seeds to different incubation time and found 45°C for 6 days maintaining 100% RH as challenging incubation period for groundnut. However, drastic reduction in seed germination was observed as the incubation period increases and the trend was similar for seed viability and seedling vigor index. Later, genetic variability for seed viability, vigor and accumulation of cytotoxic compounds was examined across groundnut genotypes upon ageing. Further, the correlation study suggest, inverse relationship between cytotoxic compounds and seed viability, germination and seedling vigor index. Accordingly, some of the genotypes namely, KCG6 and ICGV9114 were found to be susceptible to aging treatment, showing reduced seed viability, poor germination with higher accumulation of cytotoxic compounds compared to tolerant genotypes like SB3 and SB15 which showed longer seed viability that accumulated less cytotoxic compounds. Further, gene analysis of some of downstream target shows its relevance in enhancing seed viability.

Introduction

Groundnut (*Arachis hypogaea* L.) is one of the world's most important leguminous crops and an economically important oilseed crop which provides high quality edible oil (48-50%) and easily digestible protein (26-28%). For the crop establishment in the field, viable seeds are crucial input. Good quality seeds of improved varieties can contribute to about 20-25 % increase in productivity (McDonald, 1999). Therefore, there is a need to sustain seed viability during storage and improve the seedling vigor. But seed viability is a major constraint in groundnut which lasts only for few months (Sung *et al.*, 1994) and

considered to be one of the most difficult challenges to maintain.

Seed viability controlled by multiple factors such as biotic and abiotic stresses, mechanical damage as well as physiological conditions. Seed moisture content (MC), temperature, relative humidity forms the major determining factor (Ellis *et al.*, 1992). Groundnut seeds can be safely dried to very low levels of MC of 2–6% above which enhance the deterioration process (Roberts and Ellis, 1989).

Seed deterioration is an irreversible, degenerative natural process that occurs during the ageing process or under adverse environmental conditions. The deterioration of seeds during dry storage is a complex phenomenon involving changes in many seed components which accounts for 100% loss in seed vigour (Bewley and Black, 1994). Researcher over a last couple of decades showed as seed deteriorates during storage lead to the production of reactive oxygen species (ROS) and reactive carbonyl compounds (RCCs) (Foyer *et al.*, 2003). Seeds during storage are like any other dry desiccating tissue and hence expected to produce significant amount of reactive oxygen species and RCCs via lipid peroxidation and also through glycation which are highly toxic and cause damage to proteins, lipids, carbohydrates and DNA resulting in cell death (Wilson and McDonald, 1986).

These cytotoxic compounds accounts for several physiological and biochemical processes (Priestly *et al.*, 1986), which incidentally have adverse effect on crop establishment. Lipid peroxidation on seems to be the most important reason for early loss of seed viability. Apart from high temperature and relative humidity which control seed moisture content, several other environmental stresses directly or indirectly hasten up the lipid peroxidation process leading to early loss of seed viability (Wilson and McDonald, 1986).

Deterioration of seeds during storage also includes loss in protein integrity which is often described as factors that determine seed longevity. The accumulation of spontaneously damaged proteins (isoaspartyl residues) in seeds due to ageing / stress/ storage often adversely affects the seed vigour and viability (Verma *et al.*, 2013). Further, oxidative damage to DNA, formation of sugar-protein adducts cell membrane degradation, fatty acid oxidation also occur during seed deteriorated. And also, there is encountered decline in the activity of numerous enzymes and decrease in the level of antioxidants such as superoxide dismutase (SOD), ascorbate peroxidase (APX), catalase (CAT), glutathione peroxidase (GPX) and Heat Shock Proteins (HSPs) and other stress related proteins (Asada, 2006). However, in spite of several scavenging mechanisms, a small fraction of ROS escape from the scavenging systems will oxidize surrounding molecules (Bailly *et al.*, 2011). Carbohydrates and lipids targeted by ROS increases the amount of RCCs such as melondialdehyde (MDA), methyl glyoxal (MG), 3-deoxy glucosone (3-DG) are highly cytotoxic leading to production of Amadori products (Mano *et al.*, 2012) ultimately leads to production of Advanced Glycation End-products (AGEs) and Advanced Lipoxidation End products (ALEs) (Yin *et al.*, 2009). Many of these carbonyl compounds are found to be active in dry system and play an important role in deterioration of seeds.

From this context, in the present investigation, an attempt was made to(1) assess the genotypic variability for seed viability across the groundnut genotypes (2) study the relevance of cytotoxic compounds on seed viability and seedling vigor

Materials and Methods

Plant material and standardization of challenging incubation period for accelerated ageing

Twenty groundnut genotypes namely SB1, SB2, SB3, SB7, SB8, SB10, SB11, SB12, SB13, SB14, SB15, SB16, SB17, SB21, VBT1, VBT3, VBT4, VBT11, ICGV9114 and KCG6 harvested at the same season were obtained from ARS, chintamani used for the present study. Initially, accelerated ageing (AA) technique was standardized by exposing the groundnut seeds to 45 °C and 100% relative humidity (RH) for different duration. Later, it was assessed for seed viability, germination, seedling vigor index (SVI) and cytotoxic compound accumulation. For all experiments, three replications were maintained for each treatment and each replicate constituted of 10 seeds. Dry seeds of groundnut genotypes were subjected to a standardized accelerated ageing treatment of 45 °C with 100% relative humidity for 6 days. The uniform sized seeds were selected and placed in small paper cover. Seeds in paper covers were placed inside desiccators with water to maintain 100% RH and were kept inside incubator (Delouche and Baskin, 1973). After 6 days of incubation, seeds were removed from the desiccators and exposed to normal room temperature and RH overnight. Respective control seeds were maintained in normal room temperature. These seeds were then used for assessing the seed viability, germination and for quantification of cytotoxic compound

Assessing genetic variability for seed viability, germination per cent and seedling vigor index (SVI) across the groundnut genotypes upon ageing treatment

Measurement of TTC (Tetrazolium chloride) test for seed viability was adopted. Seeds of both control and aged treatment were pre-conditioned by soaking in distilled water at 28 °C for 4 h and transferred them in 1% tetrazolium chloride solution for 6 h at room temperature in dark, and then washed several times with distilled water to remove excess solution. Two hundred mg of embryos collected and incubated in TTC solution was ground in 1 ml of SDS and centrifuged at 8,000 rpm for 20 min. Later, the supernatant was collected and the extent of colour development was assessed based on OD values at 485 nm in spectrophotometer. Some amount of seeds removed from the accelerated ageing treatment and from control conditions were imbibed for 4 h and then placed in petri plates with moistened blotting paper. After two days, the percent seed germination was measured was arrived as Germination percentage = (Number of seeds germinated/ Number of seeds taken) x 100. In order to assess seedling vigour index (SVI), seedlings were maintained in petriplates for 5 more days and end of which, the root length as well as shoot length were measured and with the data of seed germination, the seedling vigor index was determined and compared with the seedlings of control treatment. SVI = Germination percentage x (root length + shoot length) (Abdul-Baki and Anderson, 1973).

Assessment of cytotoxic compounds across groundnut genotypes upon ageing treatment

Estimation of Melondialdehyde (MDA)

Excised embryos of about 100 milligram from ageing treatment and control was homogenized in 5 ml of 10% (W/V) trichloroacetic acid (HiMedia, Nasik, Maharashtra) and 0.25% of thiobarbutiric acid. The homogenate was centrifuged at 12,000 rpm for 15 min at room temperature. The supernatant was mixed with an equal

amount of thiobarbutiric acid [0.5% in 20% (W/V) trichloroacetic acid] (Sigma aldrich, Bangalore, India) and the mixture was boiled for 25 min at 100 °C followed by centrifugation for 5 min at 7,500 rpm to clarify the solution. Absorbance of the supernatant was measured at 532 nm and 600 nm and corrected for nonspecific turbidity by subtracting the absorbance at A600. The standard MDA (Sigma Aldrich, Bangalore, India) was used to develop the standard graph.

Estimation of Methyl glyoxal (MG)

MG was quantified in aged and control embryos according to Yadav *et al.,* (2005). One hundred mg of tissue was taken and ground in a known volume of distilled water and centrifuged at 11,000 rpm for 10 min at 40C and supernatant was collected. To quantify the MG content, 250 µl of 7.2 mM of 1, 2-diamino benzene (1,2-phenylenediamine), 100 µl of 5 M perchloric acid and 650 µl of the neutralized supernatant were added. The absorbance was read at 336 nm using spectrophotometer (Spectra max plus-384, Spinco Biotech pvt. Ltd., Bangalore).

Estimation of Amadori products

100 milligram sembryos of both control and aged seeds were ground in 1.2 ml of 50 mM phosphate buffer (pH 7.2). The homogenate was vortexed and centrifuged at 12,000 rpm for 15 min. Further, ammonium sulphate of 0.5 g ml-1 was added to precipitate the proteins. The pellet was dissolved in 3.3 ml phosphate buffer (50 mM, pH 7.2). Extracted proteins were used to measure the Amadori reaction products. The Amadori reaction products were measured using the nitro-blue tetrazolium (NBT) method (Wettlaufer and Leopold, 1991). To this, 1 ml of NBT reagent (0.5 mM NBT in 100 mM sodium carbonate, pH 10.3) was added to 0.2 mg of extracted proteins and incubated at 40^0C in a water bath. The absorbance at 550 nm was recorded after 10 and 20 min of incubation using spectrophotometer.

Expression analysis

Expression of downstream target genes such as Aldehyde reductase, Aldo-keto reductases1 catalase, LEA4, heat shock protein 80 (HSP80) and Protein L-iso-aspartyl methyl transferase 1 (PIMT1) were studied in contrasting genotypes after 6 days of accelerated ageing treatment. Total RNA was extracted in embryo using phenol–chloroform method according to Datta *et al.,* (1989), and cDNA was synthesized by oligo(dT) primers using Moloney murine leukaemia virus reverse transcriptase (MMLV-RT; MBI Fermentas, Hanover, MD). The cDNA pool was used as a template to perform RT-PCR analysis. The quantitative real-time RT-PCR was performed with the fluorescent dye SYBR Green (TAKARA SYBR Green qPCR Kit) following the manufacturer's protocol (Opticon 2; MJ research, USA & MJ Bioworks, Inc). The relative expression levels of the selected genes under a given stress condition were calculated using comparative threshold method. Tubulin was used as internal control for normalization.

Statistical analysis

Data recorded for different parameter under study were statistically analyzed by using analysis of variance (ANOVA).

Results and Discussion

The experiment data was recorded and the challenging incubation period for seed viability, seed germination and SVI upon accelerating ageing was standardized in different durations maintaining 45°C and

100% RH. Increase in days of incubation decelerates the seed viability (Fig. 1). There was significant decrease in seed germination from 100 to 20% as time of incubation increases from 2 to 10 days (Fig. 1). There was drastic reduction seed germination after 6 days of incubation period and the trend was similar for seed viability (reduction in TTC) and SVI (Fig. 1a, 1b and 1c). Based on the above data, 45°C for 6 days maintaining 100% RH was considered as a challenging incubation period for groundnut seed as there were approximately 73% and 70% reduction in seed germination and SVI, respectively. Further influence of accelerating ageing across the groundnut genotype for seed germination, viability and SVI was evaluated. Seeds deteriorate during the periods of prolonged storage, but the speed of deterioration varies greatly among species (Priestley, 1986). Therefore, accelerated ageing treatment has been found effective to induce faster deterioration of seeds leading to loss of early seed viability.

The data pertaining showed the effect of ageing on seed viability, germination and SVI in twenty groundnut genotypes are depicted in Table 1. It was exhibited clearly that seed viability, germination and SVI are highly sensitive to ageing treatment and the degree of sensitivity varied greatly among the genotypes (Table 1). There was up to 60% reduction in TTC on ageing treatment (Table 1). Amongst the genotype, SB3 showed higher seed germination (80%) compared ICG9114 (67 %) and KCG 6 (63 %) which showed lowest seed germination (Table 1). It appears that genotype KCG6 and ICGV9114 were highly susceptible for ageing treatment and lose viability when seed storage condition is altered even to a less extent. Similarly, ageing treatment effect SVI (Table 1). Accordingly, some of the genotypes such as KCG6, ICGV9114, SB1, SB15, SB16 and SB17 showed least SVI upon ageing treatment compared to SB13. The low vigour was due to less or failure of seed germination in those species. Remaining genotype shows intermediate character. It was also observed that, the genotypes which least reduction in TTC showed better seed germination and SVI upon ageing treatment. Reduction in TTC positively related with SVI (Fig. 2) indicating longer the viability of seed, greater the vigor index. Variation in seed germination and seedling vigor across the rice genotypes upon ageing treatment was demonstrated by Nisarga *et al.*, (2017).

There is a significant increase in production of cytotoxic compounds (MDA, MG, amadori product) in aged seeds. Amongst the genotypes, SB3 showed less accumulation of MDA followed by SB15 compared to KCG6 (Table 2). The extent of accumulation of MDA negatively correlates with seed viability (Fig. 3a), germination (Fig. 3d) and seedling vigor index (Fig. 3g). Early loss of seed viability seeds upon ageing could be due to lipid peroxidation and loss of membrane phospholipids as they are considered to be the major cause of seed ageing (Priestley, 1986; Wilson and McDonald, 1986). Similarly, genotypes ICGV9114, KCG6 and VBT11 showed higher accumulation of MG and Amodari products (Glycation End Product) compared to other genotypes (Table 3) and showed negative effect on seed viability (Fig. 3b and 3c) and germination (Fig. 3e and 3f) that also negatively effects seedling vigor index (Fig. 3h and 3i). During accelerated ageing, cytotoxic compounds like melondialdehyde, methyl glyoxal, amadori products increased with time via lipid peroxidation and glycation which results in loss in germinability (Wettlluffer and Leopard, 1991). Therefore, reduction of such cytotoxic compounds is necessary for improved seed germination in seeds. Negative relationship between cytotoxic compounds and seed viability clearly indicates that, if the

seeds remain to be viable and protect their germination ability, they need to keep cytotoxic compounds low. Accordingly, the genotypes which showed higher seed viability had least cytotoxic compound. The contrasting genotypes were identified based on the extent of cytotoxic accumulated and seed viability (reduction in TTC) as well as germination and SVI upon ageing treatment (Fig. 4). Genotypes SB3 and SB15 which showed longer seed viability that accumulated less cytotoxic compounds, and KCG6 and ICGV9114 has shorter seed viability with significantly higher levels of cytotoxic compounds upon ageing treatment were selected for gene expression studies

Table.1 Variation in seed viability, seed germination and seedling vigor index (SVI) across groundnut genotype under aged and non-aged condition

	Seed germination (%)		**Seed viability (TTC reduction) (OD @ 485nm)**		**Seedling Vigor Index (SVI)**	
Genotypes	Control	6 days AA	Control	6 days AA	Control	6 days AA
SB1	93	73	1.08	0.81	3062.3	1271.0
SB2	100	70	1.38	0.81	3665.7	1675.7
SB3	100	80	1.31	1.15	4181.0	2185.7
SB7	93	70	1.07	0.75	3118.0	1252.0
SB8	93	70	1.13	0.82	3550.0	2405.7
SB10	97	70	1.30	0.87	3133.7	2031.0
SB11	97	73	1.17	0.88	3443.3	1655.3
SB12		73	1.10	0.91	3209.0	1781.3
SB13	97	73	1.28	0.91	2674.3	2231.3
SB14	100	73	1.22	0.88	3093.7	1827.0
SB15	97	77	1.40	1.13	3934.7	1309.0
SB16	100	67	1.22	0.79	3296.7	1199.3
SB17	90	67	1.20	0.71	3539.3	1092.0
SB21	93	67	1.23	0.73	3141.0	1361.7
VB1	97	77	1.08	0.76	3248.3	1456.7
VB3	100	70	1.30	0.85	3422.7	1506.7
VB4	97	73	1.33	1.00	2692.7	1800.0
VB11	97	73	1.30	0.83	2527.3	2197.7
ICG9114	90	67	1.28	0.61	3644.0	712.0
KCG	97	63	1.25	0.56	3508.0	888.0
CD @P=0.05%						
Genotype	NS		0.17**		NS	
treatment	2.58**		0.05*		208.31*	
G*T	NS		NS		931.65**	

Table.2 Variation in accumulation of cytotoxic compound in accelerated aged and non-aged groundnut seeds

	MDA content (µM/g FW)		MG content (µM/g FW)		Amadori product (µM/g FW)	
Genotypes	Control	6 days AA	Control	6 days AA	Control	6 days AA
SB1	11.5	22.6	15.2	30.0	0.20	0.33
SB2	11.0	18.3	14.6	25.6	0.18	0.36
SB3	10.9	13.7	16.9	19.8	0.16	0.25
SB7	11.2	22.0	17.3	29.2	0.15	0.35
SB8	11.7	20.2	12.0	27.2	0.15	0.29
SB10	11.1	20.4	18.2	37.2	0.17	0.37
SB11	11.3	21.3	18.4	26.8	0.16	0.38
SB12	11.8	19.5	15.2	28.9	0.16	0.34
SB13	11.6	23.1	15.8	30.2	0.16	0.38
SB14	11.6	19.9	16.9	26.8	0.16	0.37
SB15	11.2	14.0	18.1	25.1	0.13	0.32
SB16	11.0	21.4	18.4	27.5	0.14	0.33
SB17	11.8	19.7	19.8	30.9	0.16	0.37
SB21	11.1	22.5	16.2	28.1	0.10	0.34
VB1	11.9	23.6	16.0	30.6	0.11	0.34
VB3	11.7	22.2	18.8	24.1	0.09	0.27
VB4	11.5	20.9	19.6	28.7	0.11	0.35
VB11	11.8	22.7	16.0	27.3	0.14	0.41
ICG9114	11.1	32.4	19.6	47.1	0.17	0.47
KCG	11.6	26.5	19.4	45.0	0.19	0.46
CD @P=0.05%						
Genotype	2.65**		NS		0.06**	
treatment	0.83**		2.73**		0.01**	
G*T	3.75**		NS		NA	

Fig.1 Standardization of incubation period for seed viability, germination and seedling vigor index (SVI) in groundnut upon accelerated

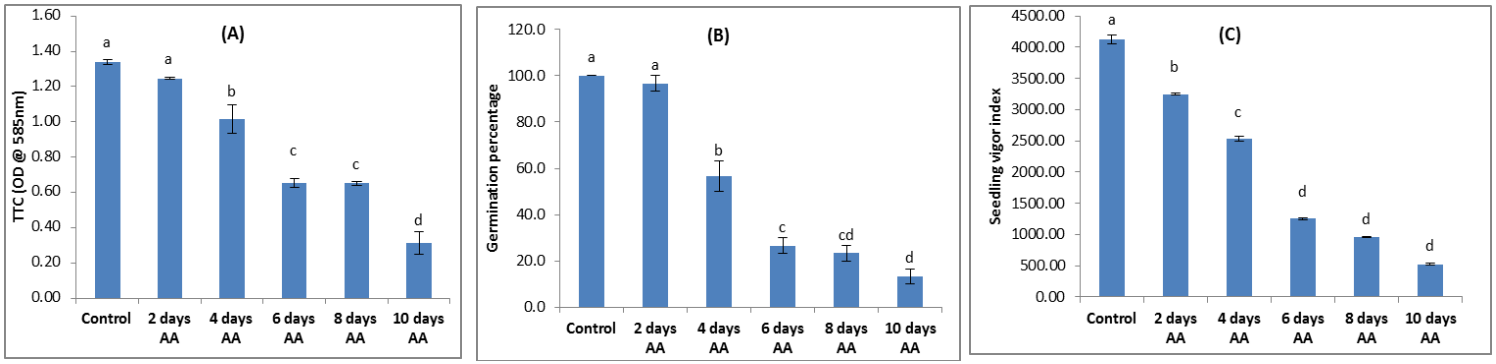


Fig.2 Relationship between seed viability and seedling vigor index (SVI) in groundnut upon accelerated aging (AA)

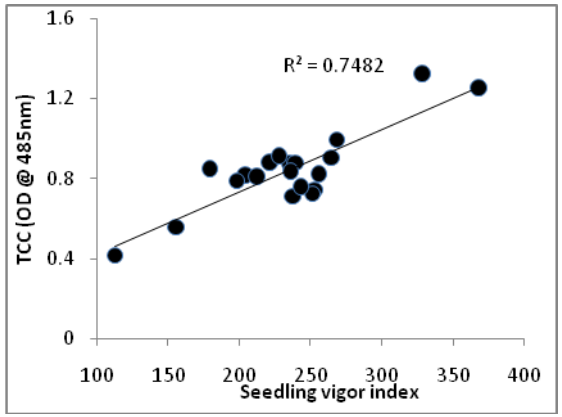


Fig.3 Accumulation of cytotoxic compounds affects seed viability, germination and seedling vigour (SVI) under accelerated ageing (AA)

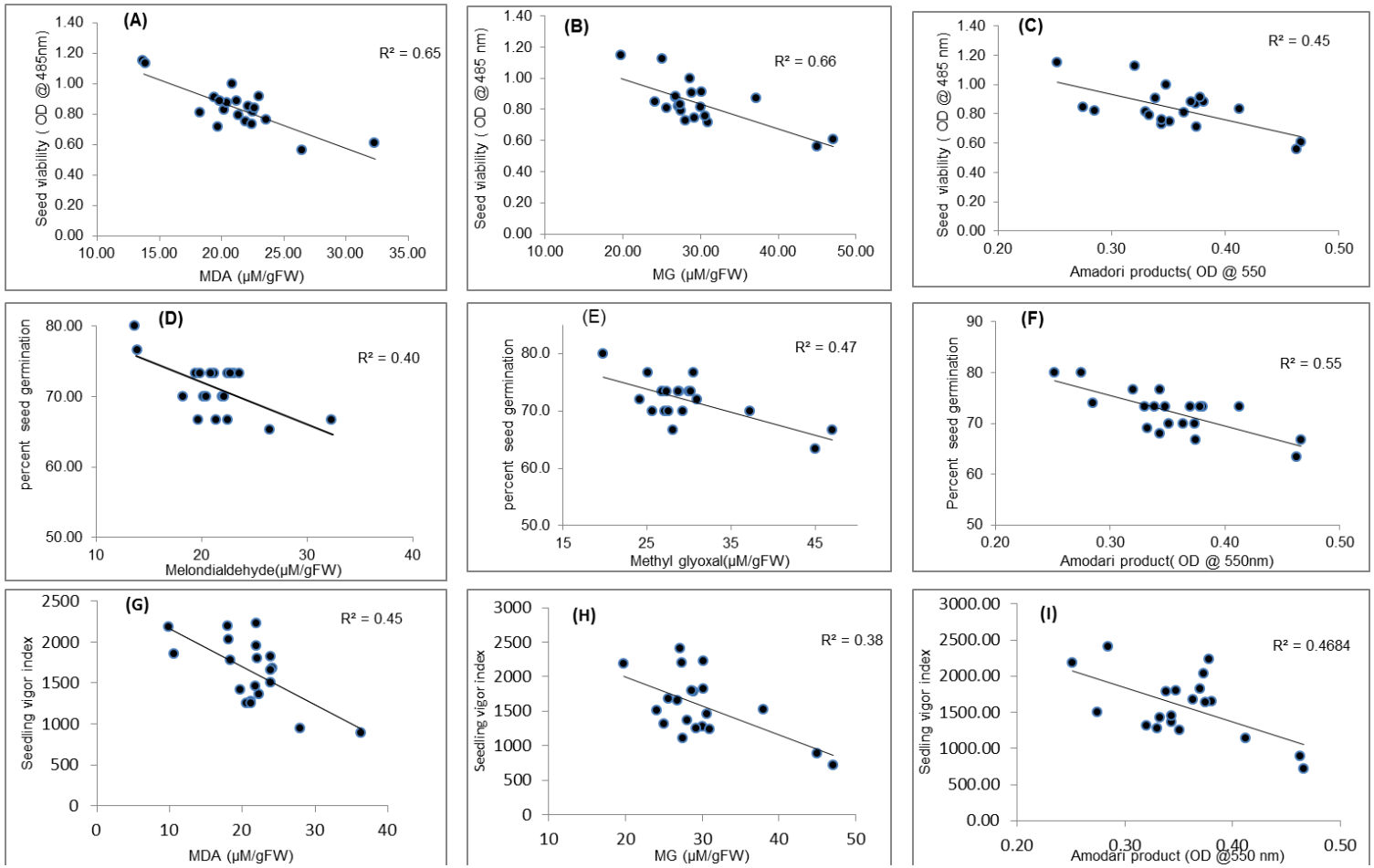


Fig.4 TTC staining (Fig. 4A) and seedling vigor index (Fig. 4B) in contrasting groundnut genotypes subjected to accelerated ageing (AA) treatment

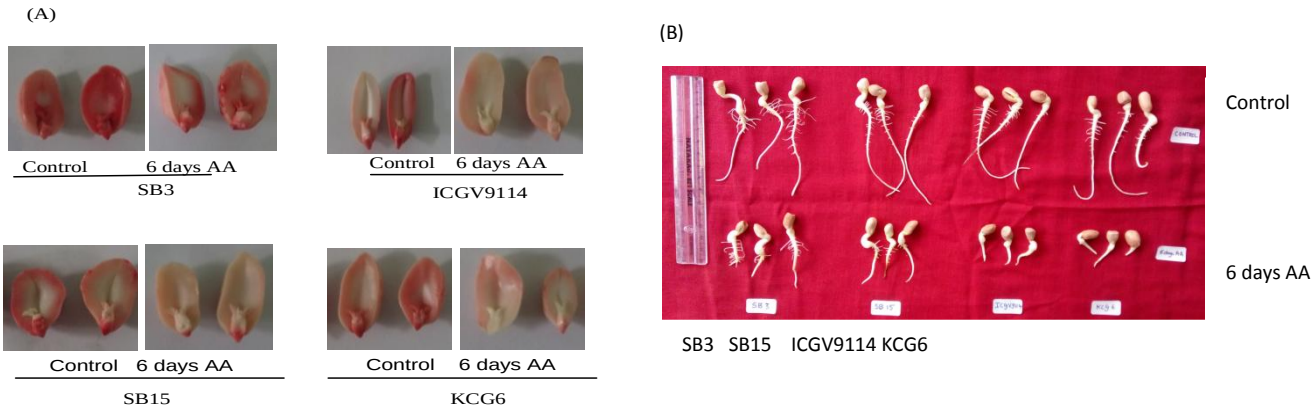
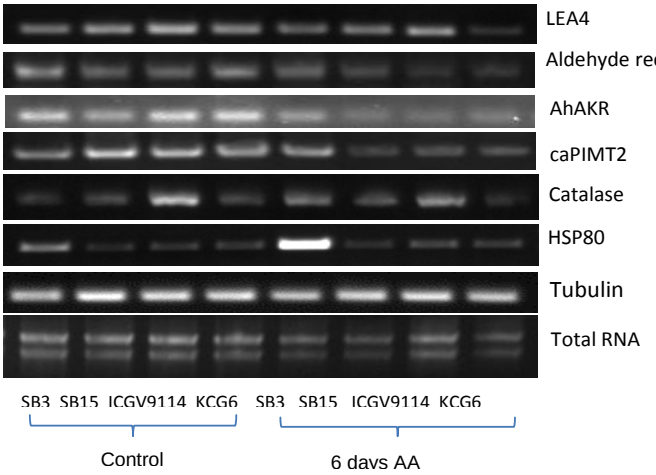


Fig.5 Expression of downstream target genes in contrasting groundnut genotypes upon accelerated ageing (AA) treatment



To assess the mechanisms associated for variability in genotypes that accumulated differential levels of cytotoxic compounds, the expression of few genes were studied. The genes that are involved in detoxification of RCC and ROS such as Aldo-ketoreductases (AKR1, Aldehyde reductase) (Oberschall *et al.*, 2000), catalase (scavenger of H_2O_2) (Mittler *et al.*, 2011) genes involved in protein stability [late embryogenic abundant (LEA4)] (Berjak *et al.*, 1997), heat shock protein 80 (HSP80)], Aldehyde reductase (Mano *et al.*, 2005) and Protein L-iso-aspartyl methyl transferase 1 (PIMT1) (Verma *et al.*, 2013) that is involved in protein inactivation were assessed in contrasting ground genotypes upon ageing treatment. The expression of all these genes was down regulated under ageing treatments (Fig. 5). The expression of HSP80 was enhanced in genotype SB3 under ageing treatment. Similarly, upon ageing expression level of LEA4, Aldehyde reductase and AhAKR1 were more in tolerant genotypes than the susceptible genotype (Fig. 5). The expression of all these genes was significantly reduced in genotype KCG6 under ageing treatment. Overall the transcript levels in all genes were reduced in ageing treatment.

In conclusion, the result of the study indicates, accelerated aging hasten up the ageing process in groundnut by increases the accumulation of cytotoxic compounds. Genetic variability for seed viability, seedling vigor and accumulation of cytotoxic compounds was observed across groundnut genotypes upon ageing treatment. Based on the levels of accumulation of cytotoxic compounds and seed viability, the contrasting genotypes were identified. Accordingly, some of the genotypes namely KCG6 and ICGV9114 were found to be susceptible to aging treatment, as they showed very less seed viability, germination percentage and accumulate higher cytotoxic compounds resulting in early loss of vigor, whereas, genotypes like SB3 and SB15 found to have high seed viability, germination with low level of cytotoxic compounds. Further, the correlation study suggest, there is inverse relationship between cytotoxic compounds accumulation and seed viability. As the cytotoxic compounds level increases, seed viability as well as seed germination decreases. Further, gene expression study confirms the role of downstream target in seed viability.

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