Positional effects on soybean seed composition during storage

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Abstract This investigation was conducted in order to determine the degree of biochemical changes during natural ageing of soybean seeds borne on different positions on stem axis. Biochemical analysis of field grown soybean seeds revealed significant differences in their oil and protein contents as a function of nodal positions. Both oil and protein content decreased after 180 days of storage (DOS) at all the nodal positions. Proportions of membrane lipids in seeds were less in basal as compared to apical positions and their proportion in stored seeds also decreased with increasing storage periods. The content of starch, total soluble sugars and reducing sugars in seeds decreased during storage for 180 days but it didn't show positional variations in their contents. The extent of lipid peroxidation increased during storage was associated with the corresponding decrease in the activities of antioxidant enzymes viz catalase and peroxidase in seeds. Seeds at basal positions showed higher rate of lipid peroxidation and lower peroxidase activity as compared to apical positions. Results suggest that soybean seeds collected from basal positions showed higher deteriorative changes during storage in comparison to apical positions that might be related to higher lipid content in seeds from basal portion of soybean stem axis as compared to apical portion.

Keywords Soybean seeds · Nodal position · Storage · Carbohydrates · Lipid peroxidation · Antioxidant enzymes

Soybean (*Glycine max* (L.) Merrill) is a high value legume having multiple importance for food, feed and industrial uses. One of the major constraints of soybean cultivation is the non availability of high vigor seeds at the time of sowing (Gupta and Aneja 2004). Seeds usually lose their germinability during period of prolonged storage (Gidrol et al. 1989) even under optimal conditions. Seed deterioration involves many biochemical and physiological changes including the loss of enzymatic activities, the loss of membrane integrity and genetic alterations, although the exact cause of seed viability loss is still not clear (Sung and Chiu 1995). During storage, seed quality can remain at the initial level or decline to a level that makes the seed unacceptable for planting purpose. This is related to many factors such as environmental conditions during seed production, pests, seed oil content, seed moisture content, mechanical damages of seeds in processing and package, air temperature and relative air humidity during storage (Guberac et al. 2003; Heatherly and Elmore 2004; Simic et al. 2004). Longevity of seed in storage is influenced by the stored seed quality as well as storage conditions. Irrespective of initial seed quality, unfavourable storage conditions, particularly air temperature and air relative humidity, contribute to accelerating seed deterioration in storage. Soluble carbohydrates generally decline with seed ageing (Petruselli and Taranto 1989) and this decline might result in limited availability of respiratory substrates for germination (Sharma et al. 2005). The lipid related changes of seeds during storage revealed decline in phospholipids and polyunsaturated fatty acids leading to marked decline in seed vigor (Priestley and Leopold 1983). Auto-oxidation of lipids and increase in the content of free fatty acids

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during storage period are the main reasons for rapid deterioration of oil seeds (Balesevic-Tubic et al. 2005). The ageing is also associated with accumulation of superoxide radical, H_2O_2 and hydroxyl radical that damage cellular membranes, enzymes and nucleic acids (Sharma et al. 2006). The protective mechanisms within the seeds involve several free radical scavenging enzymes such as superoxide dismutase, catalase and peroxidase (Sung 1996). Peroxidation of unsaturated fatty acids is considered to be one of the main reasons for poor storability of soybean seeds.

Soybean seeds borne on different nodes of the stem that vary from ground to upper part of the plant are subjected to positional effects (Bennett et al. 2003). Oil content and fatty acid composition vary between positions of seeds on the stem axis (Guleria et al. 2007, 2008). Seeds that develop in the upper one fourth of the plant contain a higher concentration of protein and lower concentration of oil than seeds from lower one fourth of the plant (Escalante and Wilcox 1993a, b). This difference in the oil and protein content at various nodal positions of the stem axis has been described to be due to variation occurring in nutrients and assimilates supply and other factors at each position. Seed filling influenced by different node position of seed influences the germination potential of seed (Sharma et al. 2009). The biochemical changes taking place during storage of seeds harvested from each position of stem axis are expected to account for low seed viability and this information will be very useful from practical point of view to plan, the harvesting of crop for seed purpose. This paper reports the biochemical analysis of the seeds located at different nodal positions of soybean stem axis at maturity and after 180 days of storage.

Materials and methods

Soybean seeds (*Glycine max* (L.) Merr. Cultivar ‘SL 295’) were procured from the Department of Plant Breeding and Genetics, Punjab Agricultural University, Ludhiana, Punjab, India. The crop was raised in the fields of Department of Plant Breeding and Genetics, Ludhiana by following the recommended Package of Practices. All the chemicals used in the present investigation were of analytical grade.

The pods were collected at maturity from each node and were separated individually, pooled and stored in paper bags for further analysis. The seeds were separated from pods from each node and were dried to a water content of ~10% on dry weight basis before storage in paper bags at ambient conditions. The seed samples from different nodal positions were drawn at 0, 90, and 180 days of storage, in triplicate and subjected to biochemical analysis. A weighed quantity of seeds was oven dried at 60 °C for 48 h to a constant weight. After drying, these seeds were immediately

placed in the desiccators before the final weighing. A portion of separated seeds was crushed and boiled in few milliliters of isopropanol to inactivate phospholipases, then homogenized in 20 volumes (w/v) of chloroform-methanol (2:1, v/v) and stored at 0–4 °C until used for lipid analysis. The extraction of lipids was done by the method of Folch et al. (1957). A suitable aliquot of lipid extract (1–2 ml) was evaporated to dryness to determine the lipid content by weighing. A portion of the tissue was put in 10 volumes (w/v) of boiling 80% ethanol and stored at 4 °C for carbohydrate analysis. 1 g of seed sample was put in 0.1 N NaOH and stored under refrigerated conditions for protein analysis. Total soluble sugar levels were determined with the phenol-sulfuric acid reagent (Dubois et al. 1956) using glucose as standard. Starch was extracted by following the method of Clegg (1956) and its content was calculated by multiplying the amount of glucose (determined by Dubois method) by a factor of 0.9. Reducing sugars content was determined by following the method of Nelson (1944). The content of phospholipids was estimated by determining phosphorus content as described by Ames (1966), glycolipids by measuring glucose content according to Roughan and Batt (1968), free fatty acids by copper complex formation as described by Lowry and Tinsley (1976) and sterols by using ferric chloride according to Zak (1957), all spectrophotometrically. The content of total glycerides was calculated by the difference of total lipid classes from 100. For malondialdehyde (MDA) determination (lipid peroxidation), 1 g seeds were hand-homogenized using 5 ml of 5% (w/v) trichloroacetic acid at 4 °C in pre-chilled mortar and pestle. The homogenate was centrifuged at 10,000 g for 20 min and the supernatant was used for MDA determination (Heath and Packer 1968). The amount of MDA present was calculated from the extinction coefficient of $155 \text{ mM}^{-1} \text{ cm}^{-1}$. The catalase and peroxidase activity was determined by homogenizing the dry seeds in 0.1 M potassium phosphate buffer, pH 7.0 containing 1% PVP. The homogenate was centrifuged at 9,000 rpm for 15 min and supernatant obtained was used to assay the activities of catalase (Aebi 1983) and peroxidase (Shannon et al. 1966). The protein was estimated by the method of Lowry et al. (1951). All analyses were carried out in triplicate and statistical analysis of the data was performed according to factorial experiment in randomized block design.

Results and discussion

Soybean seeds present at the basal nodes showed higher germination percentage whereas vigor index was higher at apical positions (Sharma et al. 2009) and germination percentage and vigor index decreased with storage period of 180 days. The dry matter content of the mature seeds

increased from basal towards the apical part of soybean stem axis and did not vary considerably during storage (Fig. 1) which might be due to enhanced mobilization of assimilates at the apical portion of the plant which is exposed to photosynthesis better than those towards the basal portion (Guleria et al. 2007). However, a small increase in dry matter content of seeds at all the positions observed from 90 to 180 DOS was similar to reported earlier (Sharma et al. 2005, 2006) which might be due to loss of moisture due to higher environmental temperature during this period.

The lipid content in mature seeds was higher at the basal position, and it decreased towards the apical position whereas protein content showed a reverse trend (Fig. 1). The lipid content decreased significantly in the seeds at all nodal positions of soybean stem axis from 0 to 180 DOS. The protein content in seeds collected from different nodal positions decreased during storage for 180 days, however, the values were still higher at apical in comparison to basal

Fig. 1 Dry matter, lipid and protein content of soybean seeds collected from various node positions of stem axis at 0 (●), 90 (■) and 180 (▲) days of storage. ($n=6$)

positions. Collins and Cartter (1956) have shown that seeds developing in the upper one-fourth portion of the plant contained higher concentration of proteins and lower concentration of oil than from lower one-fourth of the plant. Variability in protein and oil content existed among the nodes (Escalante and Wilcox 1993a; Bennett et al. 2003; Guleria et al. 2007) and these differences have been attributed to environmental factors (Wolf et al. 1982; Maestri et al. 1998). Nakasathin et al. (2000) demonstrated that the relative mobility of each nutrient at different node position generated high nitrogen to sulphur ratio in the apical position of the stem axis, which was conducive to accumulate enhanced dry matter rich in the protein subunits (Bennett et al. 2003). Correspondingly nitrogen and sulfur would be less in basal part of the plant making available the precursors for the synthesis of lipids. A decrease in oil and protein content of soybean seeds stored in different packings and temperature has been reported earlier from our laboratory (Sharma et al. 2005, 2006). This decline in lipid and protein content of seeds during storage over the fresh seeds could be attributed to increased activity of proteolytic enzymes (Roberts 1979; Mc Kersie et al. 1988). There was an increase in phospholipids (PL), glycolipids (GL) and sterols with a corresponding decrease in triacylglycerols (TAG) content from basal to apical positions of soybean stem axis (Tables 1 and 2). The proportion of PL and GL decreased during storage up to 180 days at all the nodal positions studied. Free fatty acid content (FFA) of the seeds increased during storage for 180 days and the values showed about 2 fold increases as compared to 0 day (Table 2) with higher increase in basal as compared to apical positions. At maturity, an increase in the membrane lipids such as PL, GL and sterols in the seed from basal to apical positions of stem axis suggested that the seeds were probably still synthesizing storage lipids in comparison to seeds located at basal position as observed in Indian mustard inflorescence (Munshi and Kumari 1994) and soybean (Guleria et al. 2007). This implied that the seeds were comparatively immature and synthesis of storage lipids mainly triacylglycerides were hampered due to premature senescence of seeds in apical portions. The seeds on the basal nodes acquired longer duration of seed development and optimum photoperiod to utilize carbon skeleton for lipids synthesis in preference to seeds at apical positions. An increase in the triacylglycerides during storage (Table 2) seems to be relatively due to decrease in proportions of PL, GL and sterol content (Sharma et al. 2005, 2006) presumably due to membrane disruption during storage.

The content of starch and total soluble sugars did not show much variability at different nodal positions at maturity (Fig. 2). The starch content in the seed during storage decreased from 0 to 180 days. Initially the decrease

Table 1 Changes in lipidic composition (g 100 g oil⁻¹) of soybean seeds at various node positions of stem axis during storage

Nodal position	Days of storage (DOS)								
	0	90	180	0	90	180	0	90	180
	Phospholipids			Glycolipids			Sterols		
4	0.53	0.51	0.45	9.4	6.4	5.1	2.5	3.3	2.6
5	0.52	0.52	0.42	8.9	6.5	4.9	2.4	3.3	2.2
6	0.52	0.50	0.46	11.3	7.3	4.9	2.8	2.4	2.4
7	0.55	0.52	0.47	9.1	7.1	4.8	2.3	3.4	2.5
8	0.58	0.56	0.46	10.1	6.5	4.9	2.6	2.8	2.4
9	0.59	0.51	0.47	10.8	7.2	4.6	3.0	2.9	2.3
10	0.62	0.59	0.49	9.9	7.9	4.8	2.6	2.5	2.2
11	0.6	0.58	0.52	10.8	7.3	4.8	2.7	2.9	2.2
12	0.61	0.56	0.49	11.5	7.2	4.8	3.0	2.9	2.3
13	0.58	0.55	0.52	13.8	7.3	4.8	3.5	3.0	2.4
14	0.59	0.57	0.52	11.6	7.3	4.7	3.0	3.0	2.2
15	0.6	0.57	0.51	11.3	6.8	4.7	2.9	2.8	2.1
16	0.61	0.58	0.53	10.7	7.4	4.5	3.0	2.8	2.0
17	0.6	0.57	0.51	9.8	7.5	4.5	2.6	2.4	2.0
CD ($P<0.05$) ($N=6$)	0.03	0.04	0.03	2.19	2.00	1.08	0.15	0.09	0.25

in starch content was more in basal position in comparison to apical position up to 90 DOS, however, the further decrease in starch was almost similar at all the nodal positions beyond 90 DOS. The content of total soluble sugars and reducing sugars decreased at different nodal positions from 0 to 180 days after storage except for seeds located at basal positions, where the content of total soluble

sugars showed a decline up to 90 DOS. The decrease in starch content during storage might result because of its degradation by α -amylase during storage. α -Amylase activity is known to be present in mature soybean seeds which are positively associated with the germination of soybean seeds (Thomas 1979). The decrease in the total soluble sugars and reducing sugar content may possibly be

Table 2 Changes in free fatty acids (mg 100 g⁻¹ oil) and triacylglyceride (g 100 g oil⁻¹) content in soybean seeds at various node positions of stem axis during storage

Nodal position	Days of storage (DOS)					
	0	90	180	0	90	180
	Free fatty acids			Triacylglycerides		
4	74.0	69.0	140	87.4	89.7	91.8
5	62.0	59.0	130	88.1	89.6	92.4
6	77.0	67.0	130	85.3	89.7	92.2
7	72.0	64.0	130	87.9	88.8	92.2
8	74.0	66.0	130	86.6	90.0	92.1
9	72.0	81.0	130	85.5	89.3	92.6
10	74.0	79.0	130	86.8	88.9	92.5
11	71.0	78.0	130	85.8	89.1	92.4
12	76.0	69.0	130	84.9	89.2	92.3
13	88.0	73.0	130	82.0	89.0	92.2
14	78.0	46.0	120	84.7	89.0	92.5
15	73.0	45.0	120	85.1	89.7	92.6
16	81.0	52.0	110	85.5	89.4	93.0
17	79.0	45.0	110	86.9	89.4	93.0
CD ($P<0.05$) ($N=6$)	0.10	0.10	0.11	0.81	0.82	0.91

Fig. 2 Carbohydrate composition of soybean seeds collected from various node positions of stem axis at 0 (●), 90 (■) and 180 (▲) days of storage. ($n=6$)

due to interconversion of soluble sugars into the insoluble higher oligosaccharides besides its utilization for respiration (Edge and Burris 1970). In addition, it may also be involved in the Maillard reaction to form a complex with amino acids present in the soybean seeds because soybean seeds have limited respiratory activity during storage (Vertucci and Leopold 1987).

Soybean seeds stored under ambient temperature undergo lipid peroxidation. The rate of lipid peroxidation expressed as malondialdehyde formed is an important parameter for quantifying the extent of lipid peroxidation in oil rich seeds, provided these seeds are high in linolenic acid content (Sung 1996) as are soybean seeds (Priestley and Leopold 1979). Ageing for 180 days under ambient conditions increased MDA content in seeds collected from

different nodal positions of soybean stem axis (Fig. 3). Initially the MDA levels were low in seeds from basal as compared to apical portion, however, after 180 DOS, the values were higher in seeds from basal in comparison to apical positions (Fig. 3). Gradual increase of MDA content in seed with storage period was confirmed by other authors (Priestley et al. 1980; St Angelo and Ory 1983; Balesevic-Tubic et al. 2005). Temperature and relative humidity during storage are important factors, which, besides duration of storage period affect the degree of biochemical changes in seed. The peroxidative changes in seeds from basal positions were higher as compared to apical portion since lipid content of seeds from basal portion was 3–4%

Fig. 3 Lipid peroxidation and activities of catalase and peroxidase enzymes in soybean seeds collected from various node positions of stem axis at 0 (○), 90 (■) and 180 (x) days of storage. ($n=6$)

higher in comparison to apical position (Fig. 3). These results were in accordance with results obtained by Gupta et al. (2009) who reported positional effect on MDA levels in seeds from different whorls on sunflower head.

Natural ageing not only stimulated lipid peroxidation but also depressed the activities of free radical scavenging enzymes in comparison with activities in fresh seed (Fig. 3). The peroxidase activity in the seeds from different nodal positions was higher in the basal as compared to the apical position of stem axis at maturity as well as after 180 DOS. Similarly, the catalase activity in soybean seeds decreased from harvest to 180 DOS. The catalase activity showed less variability among various positions beyond 90 DOS. However, the decline in catalase activity was higher in seeds from apical as compared to basal portion of the plant when the storage period was extended to 180 days.

The results of these studies confirm the earlier reports that the increase in the lipid peroxidation during storage is associated with a corresponding decrease in the activity of peroxidase and catalase (Sharma et al. 2005, 2006; Zhang and Kirkham 1996; Balesevic-Tubic et al. 2005). The inhibition of free radical and peroxide scavenging enzymes may result in an increase in MDA level (Sung 1996; Sharma et al. 2005). Several investigations have indicated that free radical induced lipid peroxidation can damage cell membranes and are likely to be primary cause of deterioration of aged seeds (Ponquett et al. 1992). The enhanced lipid peroxidation is also directly supported by the reduced germination percentage in the storage seeds in the present studies (Sharma et al. 2009). The higher lipid peroxidation in basal nodes during storage might be due to the fact that the removal of peroxides from these seeds might be too slow to prevent the accumulation of peroxides, thus leading to less protected situation for the soybean seeds. In the present study, the decrease in the lipid content (Fig. 1) and increase in the FFA content (Table 1) due to lipid hydrolysis in soybean seeds during storage for 180 days coincided with the increase in lipid peroxidation. These FFA are subjected to lipoxygenase leading to the formation of hydroperoxides (St Angelo and Ory 1983) and ultimately result in the accumulation of MDA (Robert et al. 1980). Thus in oilseeds such as soybean and sunflower, autooxidation of lipids and increase in the content of FFA during storage are the main reasons for rapid deterioration of seeds (Balesevic-Tubic et al. 2005).

Conclusion

Soybean seeds collected from basal portion showed higher deteriorative changes during storage in comparison to apical positions. These deteriorative changes

during storage might be related to higher lipid content in seeds from basal portion of soybean stem axis as compared to apical portion.

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