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COLD-INDUCED SWEETENING IN TUBER ENDS OF POTATO (*SOLANUM TUBEROSUM* L.) GENOTYPES

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ABSTRACT: It is a known fact that cold-induced sweetening (CIS) is produced more in tuber ends that rest of tuber parts in potatoes. But most of the studies so far have been directed to whole tuber while tuber end studies are reported very rare. In the present study, CIS is measured in tuber ends of potato genotypes, "Lady Rosetta" and "Kufri FryoM" (processing), "Kufri Sindhuri" and "MS/8 1148" (non-processing) during storage at 4° (cold) and 25°C (control) in four-way interaction experiment. Tubers were harvested after 30 d of haulm cutting and hardened in field for 10 d and then stored. Tubers were analysed at 0, 20, 40, 60 and 90 d after storage. Results found that amylases increased, and starch decreased at 4°C in non-processing genotypes only and changes were more marked in basal than apical ends. Starch decreased at earlier stages (20 and 40 d), but amylases increased throughout the storage, at 4°C. Soluble sugars increased at 4°C where glucose/ sucrose increased relatively earlier (at 20-40 d) than fructose (at 20-60 d). Increase of glucose and fructose at 4°, was higher in non-processing than processing genotypes and in basal than apical ends. However, increase of sucrose at 4°, was higher in "Lady Rosetta" and "MS/8 1148". Principal component analysis (PCA) related fructose, more closely than glucose, to amylolysis. Results indicated that sucrose synthetic/breakdown activities may be involved in CIS, and sucrose synthetic activity may relate to CIS-resistance of "Lady Rosetta".

KEYWORDS: Amylase, Fructose, Glucose, Invertase, *Solanum tuberosum* L

INTRODUCTION

Cold storage of potatoes at less than 9°C effectively extends storage life by reducing tuber respiration, fresh weight loss, disease pressure, and sprouting, but this quality is compromised by the induction of cold-induced sweetening (CIS) (Herman *et al.* 2016). CIS occurs due to the catabolism of starch to reducing sugars, glucose and fructose (Glc + Fru) (Herman *et al.* 2016). These sugars during frying serve as substrates for Maillard reaction, which gives rise to off-flavor, dark pigments, and acrylamide (probable human carcinogen) (Herman *et al.* 2016).

In the present study, four genotypes varying in CIS resistance were studied by taking tissue from tuber ends. Tuber ends are known to produce high CIS compared to other tuber parts, where basal (stem) end defect is reported to be the most common defect (Thompson *et al.* 2008). However, tuber end studies are reported less in the literature. Among four potato genotypes, "Lady Rosetta" and "Kufri FryoM" are the known processing varieties, while "Kufri Sindhuri" and "MS/8 1148" were non-processing genotypes. Work was planned at two storage temperatures, 25°, and 4° C, to know the cold-induced effect over average room temperature.

MATERIALS AND METHODS

Plant materials

Tubers of potato (*Solanum tuberosum* L.) genotypes, "Lady Rosetta", "Kufri FryoM", "Kufri Sindhuri", and "MS/8 1148", were obtained from the fields of the Department of Vegetable Science, Punjab Agricultural University, Ludhiana. Tubers were harvested

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30 days after haulm cutting and hardened in the field for the next 10 days then heaped for each genotype. From the heap of each genotype, average-sized tubers (i.e. neither too big nor too small in size) were picked randomly by observing with naked eye and packed in jute bags (about 100 tubers per bag) and stored at 4° and 25°C. Tubers were analyzed at 0, 20, 40, 60, and 90 d after storage, where 0 day was the storage day. For each measurement, four tubers per genotype were selected randomly, washed under tap water, then in distilled water, and tubers were then sliced at apical end and basal ends (approximately 1 to 1.5 cm from each end). These basal (stem) ends or apical (bud) ends were consolidated into a single sample and used for measurements in three replicates (Dhillon *et al.* 2021).

Biochemical measurements

Extraction and estimation of sugars and starch was done as given (Kaur and Zhawar 2021). Tissue (0.1 g) was extracted twice with 80% methanol, and the extract was filtered through Whatman filter paper 1. The supernatant was kept at 50-60° C to evaporate methanol, and volume was made with distilled water. This was used to estimate glucose, fructose, and sucrose. Residues were dried and used to estimate starch. Free glucose was assessed by an enzymatic method where the extract was incubated in the total volume of 2 ml containing 1.8 units of glucose oxidase, 0.6 units of peroxidase, 0.015% o-dianisidine, and 22.5% glycerol at 30° C for 90 min. Then the reaction was terminated in 1N HCL. The content was read at 540 nm and calculated using glucose standard (0.1 to 0.5 µmol). For sucrose estimation, the extract was first incubated with commercial invertase (0.25U mL^{-1}) in 0.1 M sodium acetate buffer pH 5 for one hour at 37° C, and then reaction stopped in boiling water bath for 10 min and glucose estimated as above. Free glucose value was subtracted from the invertase-treated value to calculate sucrose. Fructose was estimated by subtracting bound fructose from total fructose. Total fructose was assessed by incubating extract in 0.025% resorcinol, 23.75% ethanol, 22.5% HCL at 80° C for 20 min, and then reading at 540 nm. Standard fructose (0.1 to 0.5 µmol) was used to calculate the amount. Bound fructose was estimated after destroying free fructose in 15% NaOH at 100° C for 10 min. For starch estimation, the dried residue was incubated twice in 30% perchloric acid at 4° C, then centrifuged at 10, 000 × g for 20 min then glucose was estimated from supernatant by anthrone method (0.2% anthrone in 95% ice-cold H_2SO_4) and the value was multiplied by 0.9 to get starch value.

Amylases were estimated as given (Srivastava and Kayastha 2014). Amylases were extracted in 100 mM sodium acetate buffer pH 5.5 with 1 mM beta-mercaptoethanol and 3 mM $CaCl_2$ and 20% glycerol. Amylases were assayed in 0.8% starch, and 50 mM sodium acetate buffer pH 5.5 at 30°C where the reaction was stopped with DNS reagent, thereafter, reducing sugars were estimated by the DNS method where maltose (1-5 µmol) was used as standard.

Statistical analysis

Data were subjected to four-way factorial ANOVA in a randomized complete block design in DSAASTAT-XLX (Onofri and Pannacci 2014) to determine effects of genotype, storage temperature, duration, tuber end and their interaction. Data in the interaction were analyzed with least-squares means and separated with Fisher's least significant difference (L. S. D.) at $p < 0.05$. Multivariate analysis was done with principal component analysis (PCA). The least-square means and PCA were determined using emmeans and ggbiplot packages respectively

in RStudio (ver. 1.4.1717, Boston, MA).

RESULTS AND DISCUSSION

ANOVA result (Table 1) showed the significant effect of storage temperature, duration, genotype, and tuber ends and their interaction on sugar attributes.

Storage at 4° C is compared to 25° C (control). Only statistically significant results are presented.

Starch and amylases

Starch levels (Figure 1A) decreased at 4° by 50% in apical and 80% in basal ends of "Kufri Sindhuri" and 50% in basal ends of "MS/8 1148" at 20 d, thereafter, starch increaserd to the level of 25° in both genotypes. In "Lady Rosetta" and "Kufri FryoM", starch was not reduced rather increased 4° except in the basal end of "Kufri FryoM" at 40 d where starch decreased by 20%. Starch levels were higher in apical than basal ends at many stages in all genotypes, at 4° C. During cold storage, trend of starch was decreasing.

Amylases (Figure 1B) increased at 20 d in both ends of "Kufri Sindhuri" and "MS/8 1148" and basal end of "Kufri FryoM" while at later stages (60 and 90 d), amylases increased in all genotypes, at 4° C. The highest amylase was seen in the basal end of "MS/8 1148" at 60 d at 4° C. Amylase levels were low in "Lady Rosetta" compared to other genotypes, at 4° C at 40, 60, and 90 d. Amylase levels were higher in basal than apical ends at many stages in all genotypes at 4° C. During cold storage, amylase increased to 60 d then decreased.

The process of cold sweetening in tubers

Table 1. Analysis of variance for the effect of storage duration, storage temperature, genotype and tuber-ends and their interaction on sugar attributes of potato during post-harvest storage

Source of variation	df	MS					
		Starch	Amylase	Glucose	Fructose	Sucrose	Sucrose/Hexose
duration (D)	4	109713.7**	11908.76**	74.45**	89.44**	784.89**	5.99**
temperature (T)	1	470.8**	7802**	125.84**	67.5**	1772.67**	1.72**
T × D	4	19742.8**	1594.05**	11.06**	14.77**	139.58**	2.58**
genotype (G)	3	31973.8**	1988.74**	30.71**	1.25**	1321.24**	14.99**
G × D	12	9513**	277.3**	4.87**	6.99**	105.16**	4.9**
G × T	3	42692.9**	292.04**	0.57**	0.88**	102.87**	0.05
G × T × D	12	12131.4**	121.78**	0.49**	1.11**	26.77**	0.7**
tuber ends (E)	1	17845.2**	3.4	8.86**	0.49*	68.81**	9.07**
E × D	4	26830.4**	303.15**	5.66**	6.97**	41.94**	5.81**
E × T	1	2928.5**	547.63**	0.65**	8.7**	11.78**	2.92**
E × G	3	10575.3**	219.21**	0.28**	1.22**	7.34**	1.49**
E × D × T	4	1543.2**	93.92**	0.2**	2.09**	4.25**	0.44*
E × D × G	12	20398.5**	148.4**	0.41**	3.5**	12.27**	1.44**
E × T × G	3	1968.7**	164.94**	0.23*	2.25**	0.62	0.89**
E × D × T × G	12	986.1**	67.99**	0.22**	1.3**	2.47**	0.3**
Residual	80						
Total	239						

*, ** significant at p <0.05 or p < 0.01 respectively.

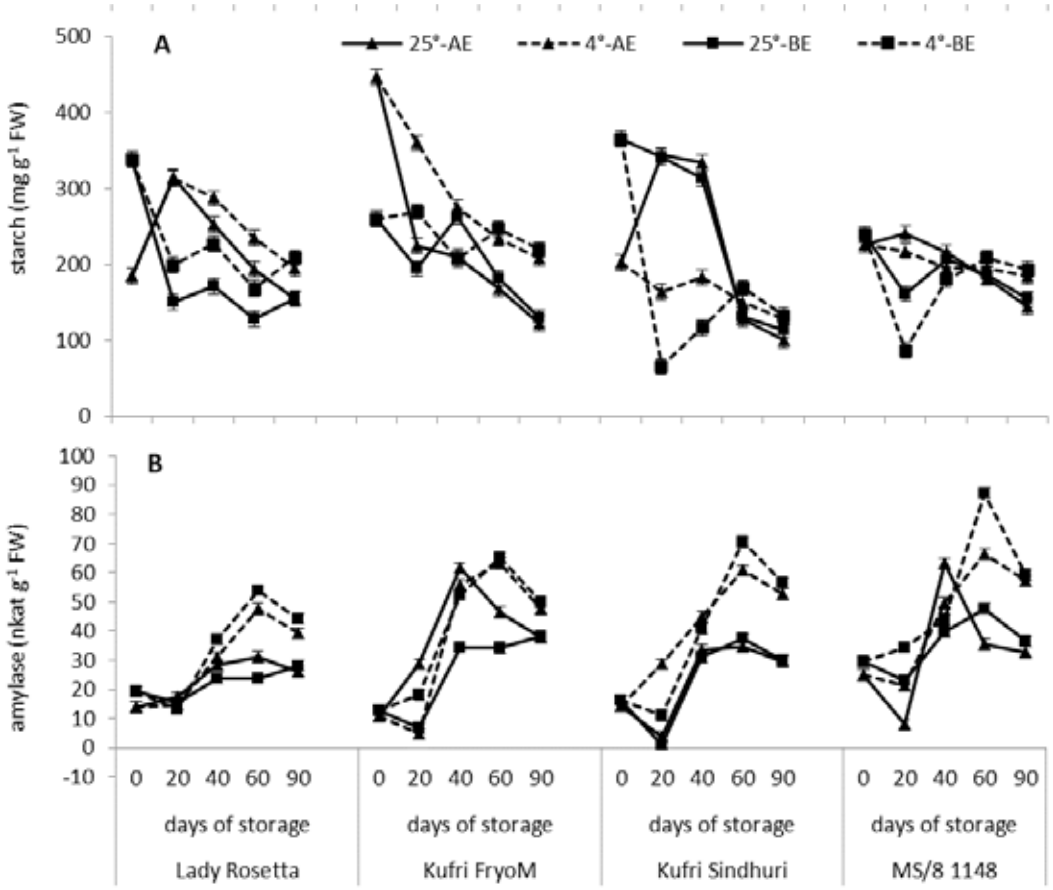


Figure 1. *Change of starch (mg g^{-1} FW) (**A**) and total amylase activity (nkat g^{-1} FW) (**B**) in tuber apical end (AE) and basal end (BE) at 0, 20, 40, 60, 90 d of storage at 25° and 4° C in potato genotypes, "Lady Rosetta", "Kufri FryoM", "Kufri Sindhuri" and "MS/8 1148". Data points are the least-square means of replicates (n = 3), and vertical bars indicate standard errors. In some instances, standard errors are small enough to be obscured by the line width.*

is reported to be based on starch mobilization in amyloplasts shown by activation of amylolytic enzymes (Zhou and Solomos 1998). Conversion of starch to reducing sugars by amylases is considered one of the main pathways in cold-induced sweetening in potato tubers (Wiberley-Bradford *et al.* 2016, Hou *et al.* 2017). The present results related cold-induced susceptibility of the genotype with starch degradation due to the gain of amylase during the early stages of cold storage. However, during late cold storage, amylases were gained by all genotypes, but starch was not reduced. Thus, starch re-synthesis might be operational during late cold storage (Sergeeva et al., 2012).

Liu *et al.* (2016) suggested that starch degradation and active transport of carbohydrates remained high in the basal ends during storage, to transport assimilates to other tuber parts during early, while sprouts during late storage. The present results found starch catabolic activity high in basal compared to apical ends during cold storage.

CIS (glucose and fructose) levels

Glucose (Figure 2A) levels were higher at 4° than 25° C at 20, 40, 60 and 90 d in all genotypes. Increase of glucose at 4°C at 20

d, was 2 to 2.5-fold in "Kufri Sindhuri" and "MS/8 1148" while 1.2 to 1.3-fold in "Lady Rosetta" and "Kufri FryoM" in basal ends. In apical ends, fold increase was 1.5 to 1.7-fold in other three genotypes while 1.3-fold in "Lady Rosetta". During cold storage, glucose trend was the increase between 0 to 20/40 d then decrease to 90 d. Glucose levels at 90 d were higher in "Kufri Sindhuri" and "MS/8 1148" than "Lady Rosetta" and "Kufri FryoM" at 4° C. The highest glucose level was seen in the apical ends of "MS/8 1148" at 20 d at 4° C. Glucose levels were seen higher in basal than apical ends at many stages of cold storage in genotypes. Results showed that glucose increased during cold exposure but decreased during acclimation. Cold induced increase of glucose was higher in non-processing than processing genotypes and in basal than apical ends.

Fructose (Figure 2B) levels were higher at 4° than 25° C at many stages in all genotypes. Increase of fructose at 4°C at 20 d, was higher in "Lady Rosetta" and "MS/8 1148" than "Kufri Sindhuri" and "Kufri FryoM" in basal ends while in apical ends, fold increase was higher in "Lady Rosetta" and "Kufri Sindhuri" than "MS/8 1148" and "Kufri FryoM". However, at 40 and 60 d, fold increase was higher in other genotypes than

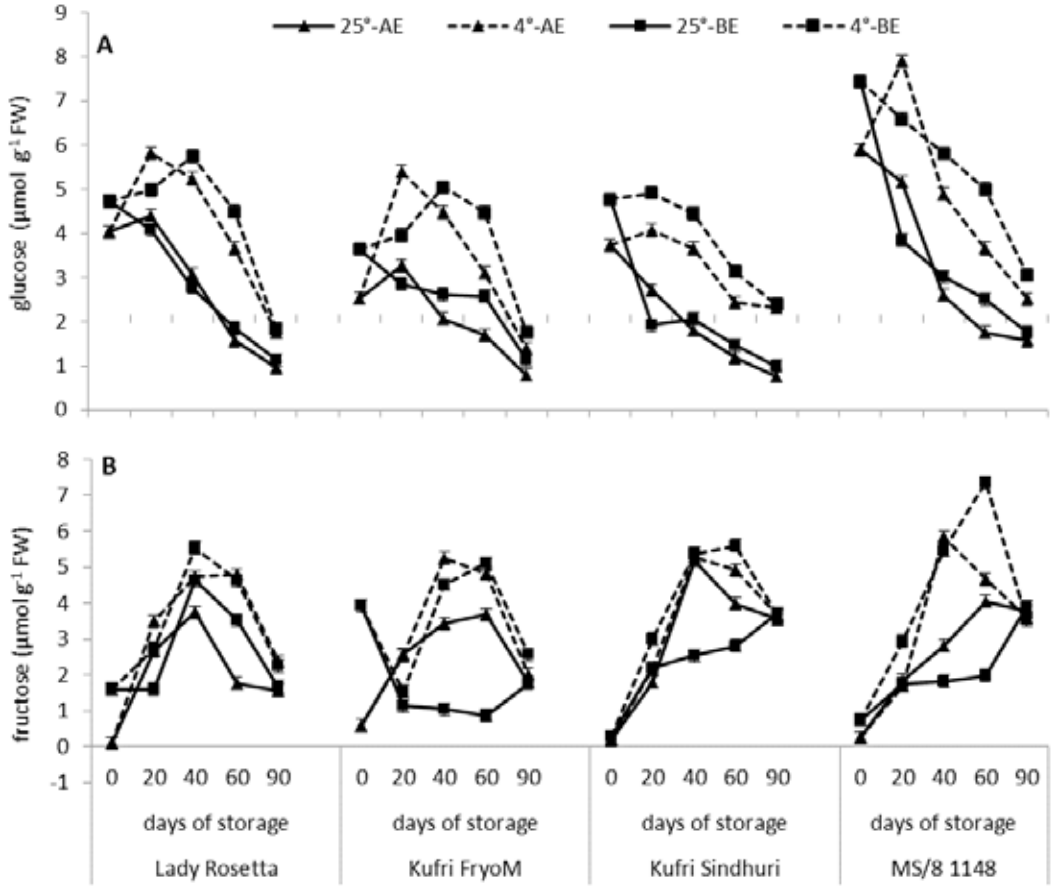


Figure 2. *Change of glucose (µmol g^{-1} FW) (***A***) and fructose content (µmol g^{-1} FW) (***B***) in tuber apical end (AE) and basal end (BE) at 0, 20, 40, 60, 90 d of storage at 25° and 4° C in potato genotypes, "Lady Rosetta", "Kufri FryoM", "Kufri Sindhuri" and "MS/8 1148". Data points are the least-square means of replicates (n = 3), and vertical bars indicate standard errors. In some instances, standard errors are small enough to be obscured by the line width.*

Lady Rosetta in basal ends. Highest fructose level was seen in the basal ends of "MS/8 1148" at 40 d at 4°C. During cold storage, fructose trend was increase till 40/60 d then decreased to 90 d. At 90 d of cold storage, fructose levels were higher in "MS/8 1148" and "Kufri Sindhuri" than "Lady Rosetta" and "Kufri FryoM". Fructose levels were higher in basal than apical ends at many stages of cold storage in genotypes. Results showed that fructose followed glucose accumulation during cold storage.

As reviewed (Thompson *et al*. 2008), CIS occurred higher in tuber basal than apical ends. The increase of amylase, glucose and fructose under cold was higher in basal than apical ends in "Kufri Sindhuri" and "MS/8 1148".

Fold increase of glucose was seen high in "Kufri Sindhuri", while CIS levels were highest in "MS/8 1148". Glucose increased by 2.6-fold in the basal end of "Kufri Sindhuri" while 1.2-fold and 1.4-fold respectively in the basal ends of "Lady Rosetta" and "Kufri FryoM" at 20 d at 4°C. "MS/8 1148" was the least dormant while "Lady Rosetta" was the most dormant genotype among eleven genotypes studied (unpublished data). Thus, high levels of sugars including sucrose can be due to the high metabolic state in "MS/8 1148" (Dhillon *et al.* 2021). "Kufri Sindhuri" was found lowest in antioxidant activity during cold storage (Dhillon *et al.* 2021), thus, sugars might be utilized at a high amount to produce stress protectants under deficiency.

Sucrose and sucrose to hexose ratio

Sucrose levels (Figure 3A) were higher at 4° than 25° C at all four stages, 20, 40, 60 and 90 d in all genotypes except basal end of "Kufri FryoM" at 20 d. Increase of sucrose at 4°, was found much higher in "Lady Rosetta" and "MS/8 1148" than "Kufri Sindhuri" and "Kufri FryoM" at 20 and 40 d. Sucrose increased by more amount in the apical end of "Kufri Sindhuri" than of "Kufri FryoM" at 20 d. Sucrose levels were seen higher in apical than basal ends in genotypes at many stages of cold storage. During cold storage, sucrose increased to 20/40 d then decreased to 90 d. Thus, sucrose accompanied glucose during cold storage.

QTL analyses have indicated the involvement of sucrose synthase (SUS), sucrose phosphate synthase (SPS), in CIS resistance (Xiao *et al.* 2018). Starch can be synthesized directly from sucrose (Baroja-Fernández *et al.* 2003). Thus, the synthesis of starch from sucrose may be the mechanism of CIS resistance in "Lady Rosetta". However, the CIS resistance of "Kufri FryoM" related to starch metabolism but not to sucrose metabolism. Low sucrose levels in "Kufri FryoM" showed that this genotype might be using sucrose breakdown direction to synthesize starch (Geigenberger 2003). Thus, the CIS resistance of "Lady Rosetta" may differ from that of "Kufri FryoM".

In potato tubers, total sugar concentrations are primarily constituted by reducing sugars (glucose and fructose) and non-reducing ones (sucrose) but unlike glucose and fructose, the role of sucrose in the browning of fried potato products is limited (Xie *et al.* 2018). Sucrose levels in potato tubers play an essential role during storage. Lessening sucrose levels through transgenic approaches had led to increased starch catabolism and respiration inside tubers during storage (Hajirezaei *et al.* 2003). A decrease in sucrose may be a signal for starch mobilization (Hajirezaei *et al.* 2003) and the onset of sprouting (Ferreira *et al.* 2017). In the present study, sucrose was seen high in "Lady Rosetta" during storage at both 4° and 25°C.

The sucrose to hexose ratio (Figure 3B) decreased at 4° C, by a large amount at

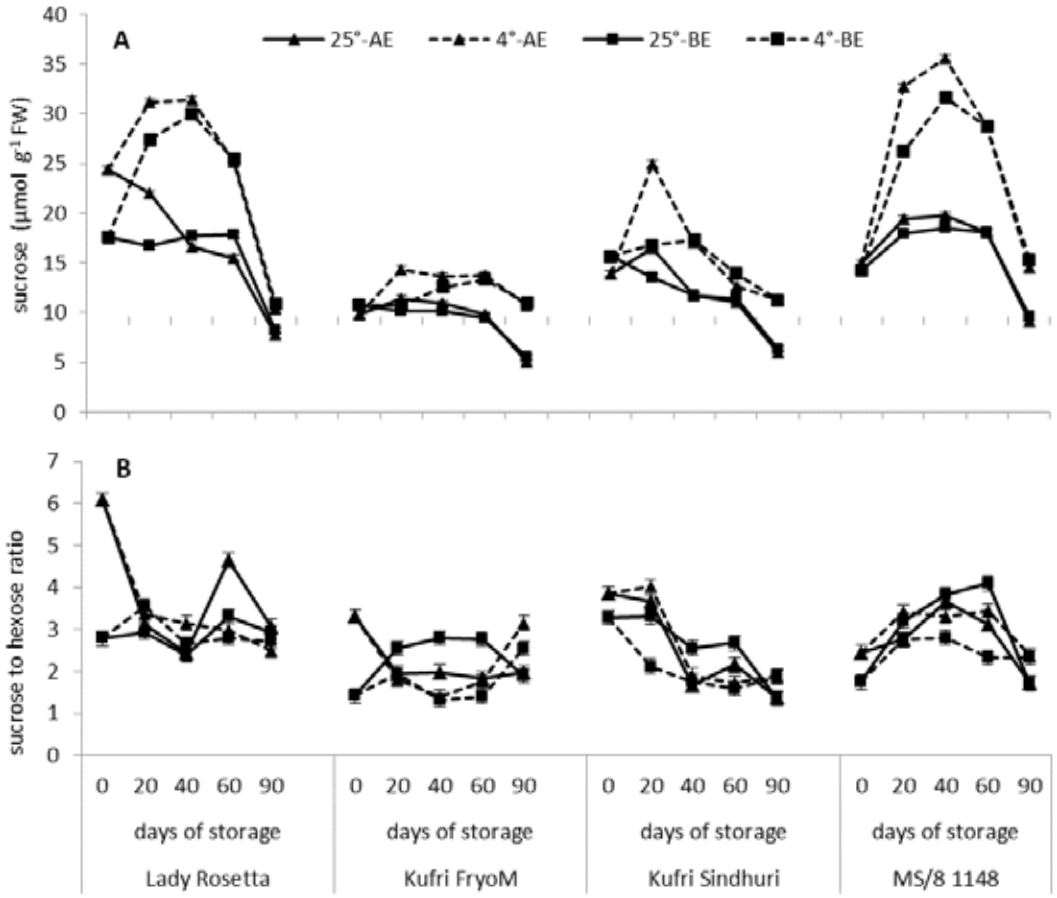


Figure 3. *Change of sucrose (µmol g^{-1} FW) (**A**) and sucrose to hexose ratio (**B**) in tuber apical end (AE) and basal end (BE) at 0, 20, 40, 60, 90 d of storage at 25° and 4° C in potato genotypes, "Lady Rosetta", "Kufri FryoM", "Kufri Sindhuri" and "MS/8 1148". Data points are the least-square means of replicates (n = 3), and vertical bars indicate standard errors. In some instances, standard errors are small enough to be obscured by the line width.*

20, 40, and 60 d in the basal ends of all genotypes except "Lady Rosetta" where the ratio decreased by a small amount at 60 d only. In apical ends, the ratio was not altered at 4° C by a large amount in all genotypes. Ratio levels at many stages were higher in apical than basal ends in genotypes at 4° C. Results showed that hexoses were oriented towards sucrose in "Lady Rosetta".

Principal component analysis (PCA)

PCA (Figure 4) explained 65.2 % variation on PC1 and PC2. Quite distinct clusters for 4° and 25° C storage were found. The cold (4° C) cluster carried high values of sucrose, glucose, fructose, amylase while the 25° C cluster had high values of starch and sucrose/hexose ratio as expected. Amylase and fructose, but not glucose, related inversely to starch. Amylase related more positively to fructose than glucose. Fructose, but not glucose, related inversely to sucrose to hexose ratios. Starch related positively to sucrose to hexose ratio. Thus, results showed that sucrose synthase (breakdown) activity might be involved in producing fructose where glucose was in bound form (UDP-glucose). And fructose accumulation might be the end-product of CIS.

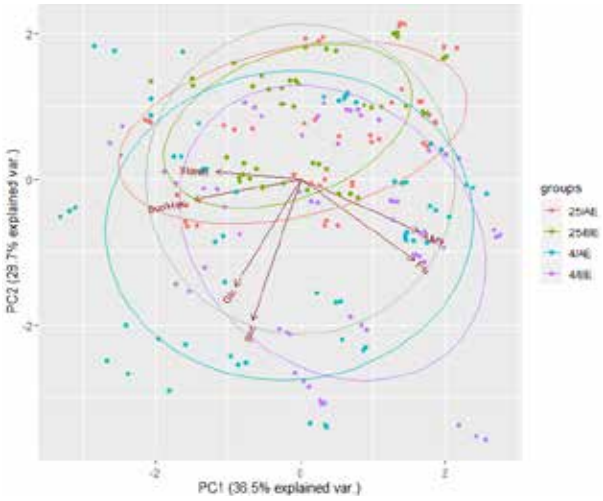


Figure 4. *Principal component analysis (PC1 and 2) performed with storage temperatures (25° and 4° C), apical and basal ends (AE and BE) of all four genotypes of all storage days (0, 20, 40, 60, 90 d).*

Acid invertase

Acid invertase activities were performed (data not shown) where enzyme activities were largely decreased at 4° compared to 25° C and only an increase was observed in the basal ends of "Kufri FryoM" and "MS/8 1148" at 20 d. A decrease in activities might be due to low metabolic activity at 4°C. Acid invertase activities were higher in basal compared to apical ends in genotypes and so was the CIS. However, activities pattern could not explain differences observed in the fructose levels among genotypes at 4°C. Invertase activities were found higher at 4° compared to 12°C storage and related to CIS-susceptibility in potato genotypes (Bandana *et al.* 2016).

This study concludes that cold-induced sweetening (CIS)-susceptibility of the genotype relates to starch degradation due to the gain of amylase during cold storage. Tuber basal ends produce more CIS than apical ends. Between tuber ends, the starch catabolic activity of the basal end relates to CIS. CIS resistance of "Lady Rosetta" may differ from that of "Kufri FryoM". Sucrose as well as starch synthetic activities may be involved in CIS-resistance of "Lady Rosetta". In the future, sucrose/starch catabolic and anabolic activities can be studied in detail in these genotypes to know more about CIS resistance.

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