Changes in sugar contents and invertase activity during low temperature storage of various chipping potato cultivars

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Abstract

Storage of tubers is vital for uninterrupted supply to potato chips/fries industry. Cold storage is preferred to maintain tuber quality. However, prolonged storage at low temperature results in cold induced sweetening (CIS) leading to sugar accumulation and browning of chips. Slowing down the CIS is of economic importance for potato industry. Screening of potatoes after cold storage for low sugar and invertase activity with exploration of best frying color was the aim of current study. Reducing sugars (RS), invertase activity and chips color were estimated after subjecting the tubers at 3°C and 7°C storage. Analytical techniques were adopted for quantification of RS and invertase activity while nine-point Hedonic scale was used for chips color evaluation. Highest invertase activity with maximum RS (mg 100-1g) and dark brown chips were observed in Kuroda following the Santé (247.83), Asterix (216.73), Crozo (193.42), Hermes (171.57) and Lady Rosetta (134.07) after storage at 3°C. Low RS were found in tubers stored at 7°C with good frying color in Lady Rosetta (98.23) followed by Hermes (104.31) and Crozo (113.27). Conclusively storage temperatures have significant effect on quality of tubers in which 7°C proved best with less RS and invertase activity having good frying color.

Keywords: quality; chips; enzyme; sugars; storage.

Practical Application: Helpful study for potato processing industry as well as for growers to get awareness about the storage behavior of various cultivars required for chips preparation.

1 Introduction

Potatoes (Solanum tuberosum L.) signify a vital staple food crop round the world. However, to maintain the quality of tuber and extend accessibility, there is a need to store the tubers for long periods often using farm level and industrial-scale facilities. Like other vegetables, low temperature storage has many advantages for consumers and growers. These include prolonged sprout dormancy, decreased rate of respiration and substantial reduction in spoilage caused by pathogens (Dale & Bradshaw, 2003; Kumar et al., 2004).

Retaining the quality of potato tubers during storage is essential for processing as well as to evade the economic loss. The processing quality of frying tubers is preferably determined by their sugar levels. (Grubben et al., 2019). Low sugar accumulations in potato tubers during storage and light chips color after frying are the key traits having significant commercial value (Dourado et al., 2019). Potato processing industries generally use RS concentration as a quality index to predict the chips color (Rodriguez-Saona et al., 1997; Amjad et al., 2017). Producing chips with consistent light-color has always been remained a challenge for potato industry. Efficient storage of tubers can regulate the supply of potatoes to the processing industry throughout the year. Low temperature storage helps in maintaining the tuber fresh weight with minimum sprouting. The only drawback associated with cold storage is CIS that results in accumulation of RS during prolonged storage. Increased levels of RS have negative influence on the quality of fried products. Surplus sugar contents react with amino acids during frying at high temperature showing unacceptable dark brown to black color chips with bitter taste and flavor (Tareke et al., 2002).

Browning of fried potato products is among the critical problems faced by potato industry in terms of waste percentage (Chuda et al., 2003). Accumulations of RS in potato tubers stored at low temperatures had been well documented previously by various researchers (Burton et al., 1992). However, the biochemical reactions involved in initiation and subsequent regulation of this mechanism is still needed to be fully explored. Activities of numerous enzymes involved in certain biochemical reactions in potato tubers during storage is closely linked to CIS. During low temperature storage of tubers, starch breaks down while sucrose is formed by UDP-glucose Pyrophosphorylase and sucrose-phosphate synthase. Sucrose is then subsequently hydrolyzed to RS by soluble acid invertase enzyme (EC 3.2.1.26), a key enzyme involved in the hydrolysis of sucrose to glucose and fructose (Mckenzie et al., 2013). Invertase facilitates the hydrolytic breakdown of sucrose into hexose monomers to fulfil the plant physiological requirements to transport carbohydrate, stress response and the sugar signalling (Roitsch & González, 2004).

Degree of sugar accumulation is also a cultivar dependent factor. It has been investigated that inactivation of enzyme phosphofructokinase (PFK) at low temperature resulted in accretion of hexose phosphates, leading to increased sucrose level (Hammond et al., 1990). The PFKs from various cultivars
with different responses illustrate diverse variations for the extent of sugar accumulation in response to low temperature storage. Zrenner et al. (1996) had observed the invertase activity in stored tubers which gradually increased at low temperatures depending on type and nature of different cultivars.

CIS arises due to disproportion between starch breakdown and sucrose metabolism, which get entry in vacuole then it might be irreversibly cleaved to hexose sugars by acid invertase (Sowokinos, 2001; Blenkinsop et al., 2004). Previous studies on carbohydrate metabolism in potatoes had shown that activities of invertase enzyme are closely related to low temperature sweetening in stored tubers (Matsuura-Endo et al., 2004). Acid invertase is a special type of enzyme, that catalyzes α-1,4 glycosidic linkage among α-D-glucose and β-D-fructose (molecules of sucrose), resulting in the release of monosaccharide such as glucose and fructose (Liu et al., 2006). Present work was attempted to elucidate the pattern of changes in sugar contents during storage at different temperatures (3 °C and 7 °C) and their relationship with invertase activity in various potato cultivars. The ultimate objective of this research work was to investigate suitable processing cultivars for chips preparation with low sugar contents and good frying color to fulfill the consumer requirements.

2 Material and Methods

2.1 Sample collection and storage

Potato tubers such as Lady Rosetta, Hermes, Santé, Crozo, Kuroda and Asterix were obtained from field. Tubers were cleaned under tap to remove the dirt and dust. Healthy and medium size tubers were selected and assigned to perforated plastic net bags for storage. Samples were dried properly at room temperature and stored separately in laboratory scale-controlled chambers (Memmert, ICH 110-260 Germany) at 3 °C and 7 °C with 80-85% relative humidity (RH) for 180 days.

2.2 Sample preparation and sugar extraction

Samples were abrasive peeled (100 g) and chopped (triplicate) taken from each cultivar stored at their respective temperatures. Mixing and homogenization of sample was conducted in methanol (80 mL) for 2 min in a blender. Homogenate treated with 5 g of carbon (activated, 70-200 mesh size) and shaken enough for 18-20 min at room temperature by bench top orbital shaker (IRMICO-OS 10, Instruments, Germany). Afterwards the homogenates were kept stored for 1.5 h at 4 °C ± 1 following the vacuum filtration (Rocker-400, Sartorius, Germany). Incubation of filtrate conducted at 37 °C for 16 h to for precipitation of proteins and then stored at 4 °C ± 1 until evaluated by HPLC.

2.3 Sample clean up and chromatographic analysis

Sample clean-up was consisted of passing it through 0.22 μm nylon filters (Minisart, Sartorius). After filtration, samples were sonicated for 25 minutes in water bath at 35 °C to eliminate air bubbles. Estimation of RS was done by HPLC (Perkin Elmer-series 200) as adopted by Kyriacou et al. (2009). HPLC was equipped with NH₂ column, (25 cm × 4.6 mm id) and refractive index detector (RID) at 214 nm wavelength. Acetonitrile and water were used with a ratio of 80:20 as mobile phase. The flow rate adjusted at 1.5 mL.min⁻¹ and column temperature kept at 40 °C.

2.4 Protein concentration

Protein concentration was calculated by Bradford method by using a standard of bovine serum albumin (BSA) along with a reagent of Coomassie brilliant blue dye (G-250). Absorbance was measured on spectrophotometer at 595 nm wavelength (Figure 1). Assays were performed in triplicate and mean values used in calculation (Bradford, 1976).

2.5 Screening of potatoes for invertase

Extraction and assay of acid invertase was performed by following the methods of Bracho & Whitaker (1990) along with some modifications as suggested by Sowokinos et al. (2000). Peeled and sliced potato sample (100 g) were taken for each cultivar and homogenized with 10 mL NaHSO₃ (0.1 M) for 2 min at 4 °C. The extract obtained was filtered through eight layers of muslin cloth. Filtrate was centrifuged at 15000 g for 35 min at 4 °C. A fraction of the supernatant dialyzed against 3-4 water changes (50-fold sample/dialysate ratio) for 2 to 3 h each. The rest of supernatant was blended for 30 min. The blended extract was centrifuged at 15000 rpm for 30 min at 4 °C and dialyzed. Precipitates formed during dialysis were decanted by centrifugation and the supernatant was assayed for invertase activity.

2.6 Assay for enzyme activity

Enzyme activity was assessed by estimating accumulated RS formed by the breakdown of sucrose. The incubation mixture of 0.5 mL was consisted of an appropriate amount of enzyme, acetate buffer (80 mM) with 143 mM sucrose at pH 4.7. Assay conducted at 37 °C temperature for 1 h. Copper reagent (0.5 mL) was added to stop the reaction. Tubers were heated instantly in boiling water bath upto 30 min. Upon cooling, arsenomolybdate reagent (0.5 mL) followed by addition of water (3.5 mL). Solutions were mixed carefully and and centrifuged for 2 min. Absorbance
was taken at 660 nm wavelength by spectrophotometer. Boiled enzyme as blanks (controlled) did not differ in absorbance compared with reagent blanks.

### 2.7 Chips making and color assessment

Five tubers were randomly selected from each cultivar, washed, peeled abrasively and cut uniformly into slices of 1.5 mm thickness by automatic slicer. The slices were washed to remove surface starch and centrifuged (PPM No. 824, Sweden) at 3000 rpm for 3 min. Dried slices were fried in a deep fryer for 3 min in pre-heated corn oil at temperature of 170 °C. Fried slices were removed, placed on plates and drained off for 1 min by centrifuging. Upon cooling the slices were taken out for color assessment. The chips color assessed under the fluorescent tube by Hedonic scale of 1 to 9 (1; darkest and 9; lightest) as adopted by Abong et al. (2010).

### 2.8 Statistical analysis

Analysis of Variance (ANOVA) was performed in triplicate by adopting Completely Randomized Design (CRD) to analyze experimental results (P<0.05) and to screen out the potential of each variety during storage by using SAS 9.1 statistical package (SAS Institute, Cary, NC, USA).

### 3 Results and Discussion

The sugar content in potato tubers differs significantly depending on the type, agroecological conditions, temperature and the duration of storage (Dramićanin et al., 2018). Sugar content and enzyme activity for six potato cultivars stored at 3 °C have been summarized (Table 1). Substantial invertase activity was present in all cultivars depending on storage temperature. High content of invertase activity was associated with protein and sugar content. Significant variations were investigated among all cultivars showing that low temperature storage stimulated invertase activity resulting in sugar accumulation. High values for invertase activity (Units.mg⁻¹) reported in cultivar Kuroda (1.009) following the Santé (0.936), Asterix (0.819), Crozo (0.871), Hermes (0.744) and Lady Rosetta (0.653), respectively.

Sugar contents for potato cultivars stored at 7 °C were concluded in Table 2. Comparatively low sugar contents were investigated at this temperature then 3 °C for all cultivars such as Lady Rosetta (98.23 mg 100⁻¹g), Santé (126.37 mg.100⁻¹g), Hermes (104.31 mg 100⁻¹g), Crozo (113.27 mg 100⁻¹g), Kuroda (138.43 mg 100⁻¹g) and Asterix (117.21 mg 100⁻¹g). Significant results (P<0.05) for invertase activity were found in the range of 0.489-0.897 Units mg⁻¹ in which higher invertase activity exhibited by Kuroda (0.897) following the Santé (0.773), Crozo (0.641), Asterix (0.635), Hermes (0.547) and Lady Rosetta (0.489) respectively.

Chips color prepared from fresh/harvest level potato tubers has been presented in Figure 2, whereas as comparative analysis of chips color from the stored tubers of 3 °C and 7 °C is depicted in Figures 3 and 4. Browning of chips as witnessed in current study has direct association with RS contents (Table 1 and 2) being observed at different storage temperatures. Significant variations (P<0.05) in color pattern of chips among all tested potato cultivars was observed after frying at constant temperature (170 °C). Frying color always remained a prime measure of potato quality for processing. It has long been associated with RS contents of stored tubers (Blenkinsop et al., 2004). Identification of compositional and metabolic factors that account for the

### Table 1. Enzyme activity* and reducing sugars of tubers stored at 3 °C. (means ± standard deviation; means carrying different letters are statistically significant)

| Potato cultivar | Total crude protein (mg) | Total activity (units) | Specific activity (units.mg⁻¹) | Reducing sugars (mg.100⁻¹g fresh weight) |
|-----------------|--------------------------|------------------------|--------------------------------|----------------------------------------|
| Lady Rosetta    | 1664.31 ± 20.0b          | 827.69 ± 6.4b          | 0.489 ± 0.07c                | 98.23 ± 1.68b                          |
| Santé           | 1367.21 ± 16.3c          | 1057.49 ± 10.8b       | 0.773 ± 0.01b                | 126.37 ± 1.5b                          |
| Hermes          | 1562.11 ± 1.5c           | 854.29 ± 5.3c         | 0.547 ± 0.03d                | 104.31 ± 1.52d                         |
| Crozo           | 1129.36 ± 3.2d           | 723.08 ± 2.0c         | 0.641 ± 0.01de               | 113.27 ± 1.72c                         |
| Kuroda          | 1859.73 ± 2.6a           | 1667.39 ± 1.1a        | 0.897 ± 0.02a                | 138.43 ± 2.18a                         |
| Asterix         | 1453.47 ± 1.1d           | 923.41 ± 1.5c         | 0.635 ± 0.03c                | 117.21 ± 1.32d                         |

*(p ≤ 0.05); (means ± standard deviation; means carrying different letters are statistically significant); *based on 1 kg tubers for each cultivar; †crude protein based on Bradford dye binding assay; ‡One unit of invertase is the amount of protein that catalyzes the breakdown of 1µmol of sucrose/min at 37 °C and pH 4.70.

### Table 2. Enzyme activity* and reducing sugars of tubers stored at 7 °C.

| Potato cultivar | Total crude protein (mg) | Total activity (units) | Specific activity (units.mg⁻¹) | Reducing sugars (mg.100⁻¹g fresh weight) |
|-----------------|--------------------------|------------------------|--------------------------------|----------------------------------------|
| Lady Rosetta    | 1873.07 ± 2.11bc         | 1223.17 ± 1.16d       | 0.653 ± 0.03e                | 134.07 ± 1.13d                         |
| Santé           | 2729.51 ± 1.54b          | 2553.61 ± 2.51b       | 0.936 ± 0.07b                | 247.83 ± 2.15b                         |
| Hermes          | 1962.13 ± 0.99d          | 1459.8 ± 1.56d        | 0.744 ± 0.04d                | 171.57 ± 1.05d                         |
| Crozo           | 1629.37 ± 2.53c          | 1419.37 ± 1.42de      | 0.871 ± 0.05c                | 193.42 ± 1.17d                         |
| Kuroda          | 2863.29 ± 3.73c          | 2889.39 ± 3.11s       | 1.009 ± 0.03s                | 397.35 ± 1.62s                         |
| Asterix         | 2672.19 ± 1.10c          | 2189.23 ± 1.99        | 0.819 ± 0.02bs               | 216.73 ± 0.96c                         |

*(p ≤ 0.05); (means ± standard deviation; means carrying different letters are statistically significant); *based on 1 kg tubers for each cultivar; †crude protein based on Bradford dye binding assay; ‡One unit of invertase is the amount of protein that catalyzes the breakdown of 1µmol of sucrose/min at 37 °C and pH 4.70.
variability in potato chips color quality among different potato cultivars has an area of interest for researchers. This recent study manifested concentration of RS in potato tubers upon storage while associated with fried chips color.

Pattern of sugar accumulation and activity of invertase enzyme in tubers stored at 7 °C was described in Table 2. The results obtained from storage at 7 °C revealed that there was gradual increase in RS along with enzyme activity but quite slow and comparatively less as compared to the tubers stored at 3 °C. It investigated that higher temperature (7 °C) was negatively associated with enzyme activity and therefore low accumulation of RS occurred. Whereas, low temperature (3 °C) activated the enzyme and hence, high sugar accumulation observed at the end of storage. Among the cultivars stored at 7 °C temperature, Lady Rosetta showed less accumulation of RS (98.23 mg 100 g fresh) with enzyme activity of 0.489 units mg⁻¹ as depicted in Table 2.

Highest RS accumulation noticed in Kuroda (138.43 mg 100 g fresh) with enzyme activity of 0.897 units mg⁻¹. Splitting of carbohydrates occurs due to the presence of invertase enzyme. It plays an important role for the hydrolysis of sucrose into fructose and glucose. Pattern of RS accumulation was diverse for all cultivars and hence, the activity of enzyme. It had well reported also by earlier studies (Karim et al., 2008) that invertase activity rises under the influence of cold storage (Sowokinos, 2001; Matsuura-Endo et al., 2004).

Assessment of chips color and overall sensory evaluation is vital quality criteria for the acceptance or rejection of processed products. The required potato products (chips/fries) must provide satisfaction and pleasure to consumers as it is a part of their eating behavior. Therefore, chips prepared from potato cultivars were assessed based on nine-point Hedonic scale with respect to their frying color as presented in Figure 5. The chips color score was assigned based on Hedonic scale.

Comparison of frying color, prepared from fresh (Figure 2) as well as stored at 3 °C and 7 °C indicated that tubers at 7 °C temperature has better chipping quality as presented (Figure 4) than tubers stored at 3 °C (Figure 3). Nine-point Hedonic scale for chips color of tubers stored at 7 °C depicted that Lady Rosetta has acceptable color score of 7.56 (golden yellow) following Hermes 6.48 (slightly yellow), Crozo 5.17 (yellow), Santé 4.79 (Yellow/brown), Asterix 3.27 (brown) and Kuroda 2.23 (dark brown) as indicated in Figures 4 and 5. On other hand, browning of potato chips after storage at 3 °C can be clearly visualized in Figure 3, showing that higher concentration of sugar contents along with invertase activity are directly proportional to chips color.

Invertase enzyme along with other proteins play a significant role in determining the sugar contents during and after the cold storage in tubers stored at low temperature (Draffehn et al., 2010). Concentration of sugars and starch present in tubers
depend on genotype as well as on the environmental factors such as storage conditions and temperature (Bhaskar et al., 2010). Storage of tubers at low temperature (3 °C) for several months leads to the conversion of starch to sugars (glucose and fructose). It was investigated that the phenomenon of COS is an adaptive response to cold stress, since sugars have been known to have an osmoprotective functions in plants (Bach et al., 2013).

Highest accumulation of RS was noticed in cultivar Kuroda (397.35 mg 100⁻¹ g) with decreasing order of 247.83 mg 100⁻¹g in Santé, 216.73 mg 100⁻¹g in Asterix, 193.42 mg 100⁻¹g in Crozo, 171.57 mg 100⁻¹g in Hermes and mg 100⁻¹g Hermes in Lady Rosetta respectively, as depicted in Table 1. Similar trends for invertase activity and sugar accumulation under the influence of low temperature and cold storage were also reported previously (25, 26, 27, 28, 29). The purpose of measuring enzyme activity was to determine the quantity of enzyme present under diverse conditions, so that the activity can be compared among different cultivars with respect to sugar accumulation during low temperature storage. Differences in sugar contents and relative activity of invertase in all cultivars have been reportedly associated with variability among starch, sugar and dry matter contents of potato tubers at harvest level (Sowokinos, 2001). Significant differences were also reported by Karim et al. (2008) for sugar contents and carbohydrate splitting enzymes levels in various indigenous cultivars next to harvesting and storage. The activities of invertase, cellulose, β-galactosidase and amylase in all varieties were increased by 2-12, 1.1-3.7, 1.9-4.5 and 1.2-4 folds, respectively from harvesting till the end of cold storage. Such enzymatic increments were responsible for carbohydrate splitting and subsequent potato sweetening.

With increasing sugar contents in cold stored tubers, the chips color turns from light brown to black upon frying at high temperature. Although enzymatic biochemical interconversion between starch and sugars are well known generally in plants and particularly in potatoes; the regulation and triggering of CIS mechanism in potato tubers is not fully understood yet (Wu et al., 2011). Furthermore, the natural variation in potato cultivars involved carbohydrate metabolism (starch to sugar) is demanding to be explored for processing industry so that suitable cultivars could be grown and stored for prolong time. Decrease in browning percentage or improvement in chips color could be attributed to decrease in RS content as these are the major components which decide the color of fried potatoes (Roe et al., 1990; Kumar et al., 2005).

4 Conclusions

The study concluded that all the cultivars showed different potential for chipping quality after cold storage with respect to sugar accumulation and enzyme activity, in which Lady Rosetta was the best cultivar with low sugars and good frying color followed by Hermes, Crozo, Santé, Asterix and Kuroda. This investigational research suggested that invertase activity has reflected various patterns of sugar accumulation in potato cultivars however; low temperature (3 °C) activated invertase activity and resulted in high accumulation of RS. On the other hand, intermediate temperature of 7 °C posed better opportunities to enhance the quality of postharvest of potato tubers with low enzyme activities, less accumulation of RS and best frying color.

References

Abong, G. O., Okoth, M. W., Imungi, J. K., & Kabira, J. N. (2010). Evaluation of selected Kenyan potato cultivars for processing into potato crisps. Agriculture and Biology Journal of North America, 1(5), 886-893. http://dx.doi.org/10.5251/abjna.2010.1.5.886.893.
Amjad, A., Randhawa, M. A., Butt, M. S., Asghar, M., Yada, R. Y., & Pinhero, R. (2017). Screening potato cultivars for low sugar accumulation during storage at various storage temperatures. *Pakistan Journal of Agricultural Sciences*, 54(2), 343-347. http://dx.doi.org/10.21162/PAKJAS/17.5062.

Bach, S., Yada, R. Y., Bizimungu, B., Fan, M., & Sullivan, J. A. (2013). Genotype by environment interaction effects on starch content and digestibility in potato (*Solanum tuberosum* L.). *Journal of Agricultural and Food Chemistry*, 61(16), 3941-3948. http://dx.doi.org/10.1021/jf3030216. PMid:23484744.

Bhaskar, P. B., Wu, L., Busse, J. S., Whitty, B. R., Hamernik, A. J., Jansky, S. H., Buell, C. R., Bethke, P. C., & Jiang, J. (2010). Suppression of the vacuolar invertase gene prevents cold-induced sweetening in potato. *Plant Physiology*, 154(2), 939. http://dx.doi.org/10.1104/pp.110.162545. PMid:20736338.

Blankinship, R. W., Yada, R. Y., & Marangoni, A. G. (2004). Metabolic control of low-temperature sweetening in potato tubers during postharvest storage. *Horticultural Reviews*, 30, 317-354.

Bracho, G. E., & Whitaker, J. R. (1990). Purification and partial characterization of potato (*Solanum tuberosum*) invertase and its endogenous proteinaceous inhibitor. *Plant Physiology*, 92(2), 386-394. http://dx.doi.org/10.1104/pp.92.2.386. PMid:16667287.

Bradford, M. M. (1976). A rapid and sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. *Analytical Biochemistry*, 72(1-2), 248-254. http://dx.doi.org/10.1016/0003-2697(76)90527-3. PMid:942051.

Burton, W. G., van Es, A., & Hartmans, K. J. (1992). The scientific basis for improvement. In P. M. Harris (Ed.), *The potato crop* (2nd ed., pp. 608-727). London: Chapman and Hall. http://dx.doi.org/10.1007/978-94-011-2340-2_14.

Chuda, Y., Ono, H., Yada, H., Ohara-Takada, A., Matsuura-Endo, C., & Mori, M. (2003). Effects of physiological changes in potato tubers (*Solanum tuberosum* L.) after low temperature storage on the level of acrylamide formed in potato chips. *Bioscience, Biotechnology, and Biochemistry*, 67(5), 1188-1190. http://dx.doi.org/10.1271/bbb.67.1188. PMid:12834309.

Dale, M. F. B., & Bradshaw, J. E. (2003). Progress in improving processing attributes in potato. *Trends in Plant Science*, 8(7), 310-312. http://dx.doi.org/10.1016/S1360-1385(03)00130-4. PMid:12878011.

Dourado, C., Pinto, C., Barba, F. J., Lorenço, J. M., Delgadillo, L., & Saravia, J. A. (2019). Innovative non-thermal technologies affecting sugar content and activity of vacuolar invertase during low-temperature storage of potato tubers from six Japanese cultivars. *Journal of Plant Research*, 117(2), 131-137. http://dx.doi.org/10.1007/s10265-003-0137-z. PMid:14986152.

McKenzie, M. J., Chen, R. K., Harris, J. C., Ashworth, M. J., & Brummell, D. A. (2013). Post-translational regulation of acid invertase activity by vacuolar invertase inhibitor affects resistance to cold-induced sweetening of potato tubers. *Plant, Cell & Environment*, 36(1), 176-185. http://dx.doi.org/10.1111/j.1365-3040.2012.02565.x. PMid:22734927.

Roe, M. A., Faulks, R. M., & Belsten, J. L. (1990). Role of reducing sugars and amino acids in fry colour of chips from potatoes grown under different nitrogen regimes. *Journal of the Science of Food and Agriculture*, 52(2), 207-214. http://dx.doi.org/10.1007/s002210052027. PMid:12878011.

Dramićanin, A. M., Andrić, F. L., Poštić, D. Ž., Momirović, N. M., & Milošković-Opšenica, D. M. (2018). Sugar profiles as a promising tool in tracing differences between potato cultivation systems, botanical origin and climate conditions. *Journal of Food Composition and Analysis*, 72, 57-65. http://dx.doi.org/10.1016/j.jfca.2018.06.005.

Grubben, N. L. M., Witte, S. C. M., & Keessman, K. J. (2019). Postharvest quality development of frying potatoes in a large-scale bulk storage facility. *Postharvest Biology and Technology*, 149, 90-100. http://dx.doi.org/10.1016/j.postharvbio.2018.11.001.

Hammond, J. B., Burrell, M. M., & Kruger, N. J. (1990). Effect of low temperature on the activity of phosphofructokinase from potato tubers. *Planta*, 180(4), 613-616. http://dx.doi.org/10.1007/BF02411461. PMid:24202108.

Karim, M. R., Khan, M. M. H., Uddin, M. S., Sana, N. K., Nikkon, F., & Rahman, M. H. (2008). Studies on the sugar accumulation and carbohydrate splitting enzyme levels in post harvested and cold stored potatoes. *Journal of Bio-Science*, 16, 95-99. http://dx.doi.org/10.3329/jbs.v16i6.3748.

Kumar, D., Paul, V., & Ezekiel, R. (2005). Chipping quality of potatoes stored in heaps and pits in subtropical plains of India. *HortScience*, 32(1), 23-30.

Kumar, D., Singh, B. P., & Kumar, P. (2004). An overview of the factors affecting sugar content of potatoes. *Annals of Applied Biology*, 145(3), 247-256. http://dx.doi.org/10.1111/j.1744-7348.2004.tb00380.x.

Kyriacou, M. C., Siomos, A. S., Ioannides, I. M., & Gerasopoulos, D. (2009). The chip-processing potential of four potato (*Solanum tuberosum L.*) cultivars in response to long-term cold storage and reconditioning. *Journal of the Science of Food and Agriculture*, 89(5), 758-764. http://dx.doi.org/10.1002/jsfa.3509.

Liu, C. C., Huang, L. C., Chang, C. T., & Sung, H. Y. (2006). Purification and characterization of soluble invertases from suspension-cultured bamboo (*Bambusa edulis*) cells. *Food Chemistry*, 96(4), 621-631. http://dx.doi.org/10.1016/j.foodchem.2005.02.044.

Matsuura-Endo, C., Kobayashi, A., Noda, T., Takigawa, S., Yamauchi, H., & Mori, M. (2004). Changes in sugar content and activity of vacuolar acid invertase during low-temperature storage of potato tubers from six Japanese cultivars. *Journal of Plant Research*, 117(2), 131-137. http://dx.doi.org/10.1007/s10265-003-0137-z. PMid:14986152.

McKenzie, M. J., Chen, R. K., Harris, J. C., Ashworth, M. J., & Brummell, D. A. (2013). Post-translational regulation of acid invertase activity by vacuolar invertase inhibitor affects resistance to cold-induced sweetening of potato tubers. *Plant Cell & Environment*, 36(1), 176-185. http://dx.doi.org/10.1111/j.1365-3040.2012.02565.x. PMid:22734927.

Rodrigue-Saona, L. E., Wrolstad, R. E., & Pereira, C. (1997). Modeling the contribution of sugars, ascorbic acid, chlorogenic acid and amino acids to non-enzymatic browning of potato chips. *Journal of Food Science*, 62(5), 1001-1010. http://dx.doi.org/10.1111/j.1365-2621.1997.tb15024.x.

Suddenly, the sentence “Processing quality of stored tubers” appears in the text. It is unclear how it relates to the rest of the text. It might be a placeholder or an error.