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Sweetening During Low-Temperature and Long-Term Storage of Indian Potatoes

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Abstract The aim of the present research was to study potato storage behaviour in terms of lipid peroxidation and starch hydrolysis in three cultivars differing widely in storability. Popular potato cultivars among Indian farmers, namely Kufri Chipsona-1, Kufri Jyoti and Kufri Pukhraj with good, medium and average storability, respectively, were evaluated during storage at 4 and 12 °C for 180 days. Both low-temperature and long-term storage increased the reducing sugar and sucrose content and this increase was significantly higher at 4 °C compared to 12 °C. Contents were highest in Kufri Pukhraj, followed by Kufri Jyoti, and lowest in Kufri Chipsona-1. Malondialdehyde content and catalase activity were also higher at 4 °C in all the three cultivars. Malondialdehyde content was highest in Kufri Pukhraj followed by Kufri Jyoti and Kufri Chipsona-1, whereas catalase and peroxidase activities were highest in Kufri Chipsona-1 and lowest in Kufri Pukhraj. Kufri Chipsona-1 possessed the highest resistance to activated oxygen due to high catalase and peroxidase levels, and also maintained the lowest malondialdehyde and sugar contents and the best chip colour of the three cultivars studied. These features make this cultivar superior for processing purposes.

Keywords Catalase · Lipid peroxidation · Malondialdehyde · Peroxidase · Potato tubers · Reducing sugars · Storage

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Introduction

Potatoes are stored at low temperatures to maintain a year-round supply. Long-term storage of potatoes at elevated temperatures (12 °C) generally leads to the so-called senescent sweetening whereas storage at low temperatures (< 7 °C) leads to 'low temperature sweetening', both resulting from the conversion of starch to sugars. Loss of membrane integrity during ageing due to increased lipid peroxidation caused by built up of free radicals (Gill and Tuteja 2010) and changes in amyloplast membrane structure (O'Donoghue et al. 1995) are involved in both types of stresses. As the lipid peroxidation progresses during ageing and low-temperature storage, malondialdehyde (MDA) content, a sensitive marker of lipid peroxidation and membrane damage, starts accumulation in the cells (Dipierro and Leonardis 1997).

Various antioxidant systems have been studied as possible defences against free radical-mediated damage during ageing and low-temperature storage (Spychalla and Desborough 1990b; Kumar and Knowles 1993). Low-temperature storage and time-dependent increases of enzymatic antioxidants such as superoxide dismutase and catalase (Spychalla and Desborough 1990b), as well as non-enzymatic antioxidants such as phenols (Reddivari et al. 2007), have been reported. These increases were correlated with the reported increase of lipid peroxidation in potato tubers and thus with increased production of reactive oxygen species.

The quality of potato tubers for fresh market or processing out of storage depends greatly upon the cultivar and storage conditions, including length of storage period. Seed tubers are generally stored at 2–4 °C in commercial cold stores at about 95% relative humidity. These potatoes are not suitable for table and processing purposes, as potatoes stored at these temperatures accumulate high concentrations of reducing sugars and become sweet in taste. Besides, due to high sugars, these potatoes produce dark-coloured chips which are unacceptable to consumers. Potato tubers with high sugar content are undesirable in the processing industry as the fried products prepared from these potatoes are dark in colour and bitter in taste due to the 'Maillard reaction' that occurs between reducing sugars and nitrogenous compounds at high frying temperatures (Kumar 2011). Table and processing potatoes are generally stored at 10–12 °C after treating the potatoes with sprout suppressant for long-term storage (Singh et al. 2014). Therefore, commercially stored potato tubers are commonly held between 2 and 12 °C for up to 6–7 months.

Based on their importance, Indian potato cultivars Kufri Jyoti, Kufri Pukhraj and Kufri Chipsona-1 were used in this study. Cultivar Kufri Jyoti occupies almost 30% of potato area in India, whereas cultivar Kufri Pukhraj occupies almost 10% of the cultivated area. Kufri Jyoti is a medium-maturing cultivar and is the most popular potato cultivar widely adapted in hills, plains and plateau. Kufri Pukhraj being an early-maturing cultivar provides remunerative prices to farmers before the normal harvest season. Kufri Chipsona-1 is being grown on a large scale by the potato processing industry. This variety yields processing grade tubers and has good resistance to late blight. Kufri Chipsona-1 is well adapted to Indo-Gangetic plains (Luthra et al. 2008).

The extent of activated oxygen damage to Indian potato cultivars during low-temperature and long-term storage is not known and quantification of this damage in plant tissues is difficult. However, it is easier to quantify endogenous antioxidants, which detoxify potentially damaging forms of activated oxygen. Enzymatic and non-

enzymatic antioxidants catalase, peroxidase and total phenol were assessed along with malondialdehyde and sugar contents in the three potato cultivars (varying widely in storability) stored at 4 and 12 °C for 180 days to define cultivar-dependent differences in activated oxygen damage.

Materials and Methods

The experiment was conducted at the Central Potato Research Institute, Shimla, during 2011–2012 and 2012–2013. Freshly harvested tubers of three potato cultivars varying widely in keeping and processing quality, namely Kufri Chipsona-1 (good), Kufri Jyoti (medium) and Kufri Pukhraj (average) (Mehta and Ezekiel 2010), were used in this study. The tubers came from the crop raised at CPRIC, Modipuram, India (29° 4′ N, 77° 46′ E, 237 masl) using standard agronomic practices. The crop was planted at Modipuram consecutively for 2 years in the last week of October (on the 25th of October) and harvested after 120 days except for Kufri Pukhraj which was harvested at 90 days. After skin maturity, tubers were transported to Central Potato Research Institute, Shimla. Samples of 10 kg of each of the three cultivars were stored in three replicates at 4 ± 0.5 °C (walk-in chamber, Vista Biocell, India) and at 12 ± 0.5 °C (walk-in chamber, Vista Biocell, India) for 6 months (180 days). Potatoes stored at 12 °C were treated twice with 35 ml/tonne of CIPC (50% active ingredient of commercial formulation from M/s United Phosphorous Limited, Mumbai, India) (Ezekiel et al. 2005). Two tubers from every 10 kg bag were taken from both the storage chambers at periodic intervals, and in total, six tubers were used for each biochemical analysis. Biochemical analysis was done before storage and after 90 and 180 days of storage (DOS) following standard methods in three replications. Reducing sugar content was quantified by Nelson arsenomolybdate reagent (Somogyi 1952), sucrose by anthrone solution (Van Handel 1968) and total phenols by Folin-Ciocalteu phenol reagent (Malik and Singh 1980).

Catalase Activity

The catalase activity was determined using the methodology proposed by Aebi (1983). Fresh tuber tissue (0.5 g) was homogenised in 5 ml of ice-cold 0.05 M phosphate buffer, pH 7.5. Samples were centrifuged at 10,000 rpm for 20 min at 4 °C and supernatant was collected. The activity was carried out in a reaction mixture containing 1 ml H_2O_2 solution (0.2 ml H_2O_2 diluted to 50 ml with sodium phosphate buffer, pH 7.5) and 1.8 ml sodium phosphate buffer, pH 7.5. To this, 0.1 ml enzyme extract was added and absorbance was immediately recorded for 2 min at 15-s intervals at 240 nm on a UV-Vis spectrophotometer.

Peroxidase Activity

Peroxidase activity was measured using the methodology proposed by Shannon et al. (1966). Tuber tissue (1 g) was homogenised in 5 ml of ice-cold 0.1 M chilled phosphate buffer (pH 6.5) and centrifuged at 10,000 rpm for 20 min at 4 °C. Supernatant was collected and the volume was raised to 3 ml with extraction buffer. In a

spectrophotometric cuvette, 3 ml 0.05 M guaiacol containing 0.1 M phosphate buffer (pH 6.5) and 0.1 ml enzyme extract was used. Reaction was initiated by adding 0.1 ml of 0.8 M hydrogen peroxide and reading was immediately recorded for 3 min at 15-s intervals at 470 nm.

Malondialdehyde Content

Malondialdehyde (MDA) content was estimated by the method described by Stewart and Bewley (1980). Tuber tissue (0.5 g) was extracted in 5 ml of distilled water and 5 ml of thiobarbituric acid reagent (0.5% thiobarbituric acid in 20% trichloro-acetic acid). Samples were incubated at 95 °C for 2 h and reaction was stopped by putting the tubes in an ice bath for 20 min. Samples were centrifuged at 10,000 rpm for 1 h and absorbance of the supernatant was measured at 532 and 600 nm. The nonspecific absorbance of the supernatants at 600 nm was subtracted from the absorbance at 532 nm. The MDA equivalent was calculated on the resulting difference using the extinction coefficient of 155 mM^{-1} cm^{-1}.

Statistical Analysis

A completely randomised design was followed with each treatment having three replications. The data were analysed using MSTAT 4.0C software and the procedure of Gomez and Gomez (1984). Differences between means were compared using Tukey's test ($P < 0.05$). Different letters have been used to indicate significant differences between the cultivars ($P < 0.05$).

Results and Discussion

Sugar and Malondialdehyde Accumulation During Low-Temperature and Long-Term Storage

The effect of storage duration, storage temperature, cultivar and interaction between these three parameters on reducing sugars and sucrose content was significant. Reducing sugar and sucrose contents before storage were significantly higher in Kufri Pukhraj, and differences between Kufri Chipsona-1 and Kufri Jyoti were non-significant (Figs. 1 and 2). Reducing sugar content was 455, 200 and 180 mg/100 g FW and sucrose content was 114, 71 and 69 mg/100 g FW in Kufri Pukhraj, Kufri Jyoti and Kufri Chipsona-1, respectively. The reducing sugars in freshly harvested tubers of Kufri Chipsona-1 were comparatively higher than the content required for processing (i.e. 0.1%), although Kufri Chipsona-1 is a variety which is very well known for processing attributes. Sugar accumulation at both the storage temperatures increased with the increase in storage duration and the increase was more at 4 °C throughout the storage period, and the magnitude of accumulation was high for Kufri Pukhraj. Thus, cultivars differ in their susceptibility to low temperature and senescent sweetening. Reducing sugars decreased slightly after 90 DOS at 12 °C due to decreased invertase activity. However, reducing sugar content was 1077, 995 and 712 mg/100 g FW and sucrose content was 620, 556 and 472 mg/100 g FW in Kufri Pukhraj, Kufri Jyoti and

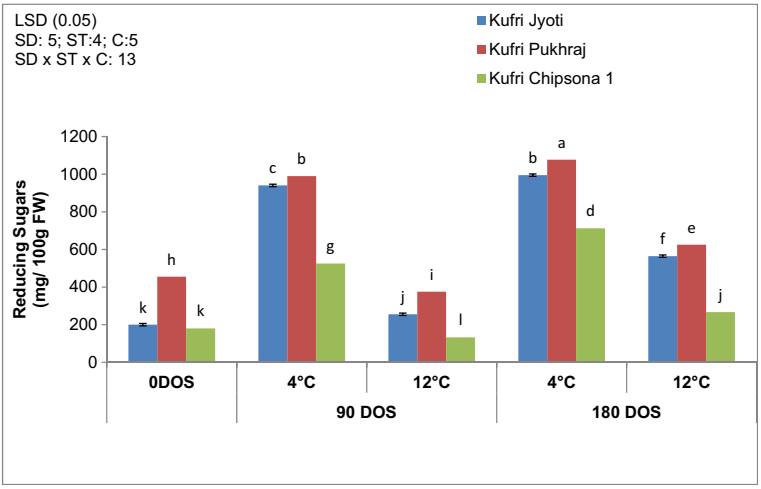

Fig. 1 Changes in reducing sugar content (mg/100 g fresh weight) in the three potato cultivars during low-temperature storage [Mean separation has been done using Tukey's test. Different letters indicate significant differences between cultivars ($P < 0.05$). Standard error bars represent standard error of interaction between storage duration, temperature and cultivar] (*SD* storage duration, *ST* storage temperature, *C* cultivar, *DOS* days of storage)

Kufri Chipsona-1, respectively, after 180 DOS at 4 °C. Sugar contents were high in Kufri Pukhraj and low in Kufri Chipsona-1, before as well as after storage. Low levels of sugars in Kufri Chipsona-1 makes it suitable for processing purposes. As expected, sucrose accumulation was greater than that of glucose and fructose during storage (Wismer et al. 1998; Barichello et al. 1990). The enzyme sucrose phosphate synthetase has been reported to play an important role in sucrose formation. The resultant sucrose

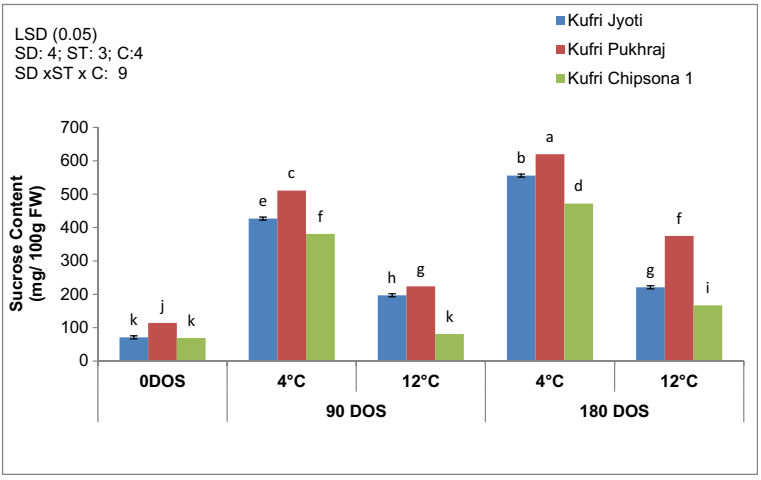

Fig. 2 Changes in sucrose content (mg/100 g fresh weight) in the three potato cultivars during low-temperature storage [Mean separation has been done using Tukey's test. Different letters indicate significant differences between cultivars ($P < 0.05$). Standard error bars represent standard error of interaction between storage duration, temperature and cultivar] (*SD* storage duration, *ST* storage temperature, *C* cultivar, *DOS* days of storage)

acts as a substrate for vacuolar acid invertase, resulting in accumulation of glucose and fructose. Results corroborate the earlier findings of higher accumulation of reducing sugars in Kufri Pukhraj as compared to Kufri Chipsona-1 and higher increase in reducing sugar contents at 4 °C as compared to higher storage temperature (8–25 °C) (Spychalla and Desborough 1990a; Kumar 2011; Kumar et al. 2012; Freitas et al. 2012). As expected, sucrose content was also higher in potato tubers stored at 4 °C as compared to 12 °C (Wismer et al. 1998). Higher increase in reducing sugars at 4 °C could be due to higher invertase activity and decreased respiration rate along with an increase in activity of starch hydrolysis enzymes (Duplessis et al. 1996; Sowokinos 2001).

As mentioned in the Introduction, malondialdehyde (MDA) content is a sensitive marker of lipid peroxidation and membrane damage. MDA content was highest in Kufri Pukhraj (0.204 nmol ml^{-1}), followed by Kufri Jyoti (0.070 nmol ml^{-1}), and lowest in Kufri Chipsona-1 (0.053 nmol ml^{-1}) (Fig. 3). MDA content increased up to 180 DOS and the increase was significantly higher at 4 °C as compared to 12 °C in all the cultivars, indicating a higher level of lipid peroxidation at low temperature and under ageing stress. The content of MDA after 180 DOS was 2.18, 1.86 and 1.59 nmol ml^{-1} at 4 °C and 1.95, 1.79 and 1.36 nmol ml^{-1} at 12 °C in Kufri Pukhraj, Kufri Jyoti and Kufri Chipsona-1, respectively. A higher level of MDA was reported at 3 °C than at 9 °C up to 40 weeks of storage by Dipierro and Leonardis (1997). Lipid peroxidation, which is the main cause of membrane deterioration, has previously been shown to increase at low temperature (Dipierro and Leonardis 1997) and with advancing age (Afify et al. 2012).

Kufri Pukhraj is a very popular cultivar among Indian farmers. However, performance of Kufri Pukhraj is not good during long-term storage and weight loss is almost 10%, which is not acceptable for marketing. MDA, which is a product of lipid peroxidation, was high in cultivar Kufri Pukhraj at all stages of storage. Lipid peroxidation generally takes place when reactive oxygen species reach above a threshold

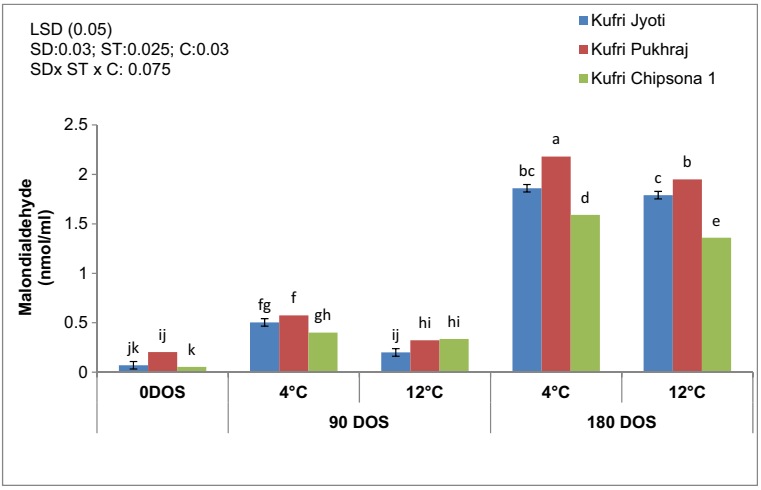

Fig. 3 Changes in malondialdehyde content (nmol/ml) in the three potato cultivars during low-temperature storage [Mean separation has been done using Tukey's test. Different letters indicate significant differences between cultivars ($P < 0.05$). Standard error bars represent standard error of interaction between storage duration, temperature and cultivar] (*SD* storage duration, *ST* storage temperature, *C* cultivar, *DOS* days of storage)

level. The results for malondialdehyde have shown that this cultivar is very prone to lipid peroxidation and hence, not suitable for long-term storage. This is important information for the storage industry, since cultivar Kufri Pukhraj occupies about 10% of the total cultivated area in the country.

In accordance with already published results (Kumar and Knowles 1993), trends in MDA and reducing sugar concentrations with advancing age were similar (Figs. 1 and 3). The accumulation of reducing sugars during prolonged storage of potato tubers (referred to as 'senescent sweetening') is most likely due to progressive degeneration of amyloplast membranes (Sowokinos et al. 1987), which facilitates the enzymatic hydrolysis of starch. The age-induced loss of amyloplast membrane integrity may thus be due to gradual peroxidation of amyloplast membrane lipids. Low temperature also induces a similar effect on the amyloplast membrane as those induced by ageing. The mechanism of membrane damage is similar under both types of stresses. Cultivar Kufri Chipsona-1, having the lowest sugar and MDA contents, appeared to be more resistant to cold-induced sweetening as well as senescent sweetening.

Activation of Enzymatic and Non-enzymatic Antioxidants

Interaction between storage duration, storage temperature and cultivar with respect to phenol content was non-significant. Total phenol content in potato tubers tends to increase during storage as reported earlier (Freitas et al. 2012). The total phenol content was highest in Kufri Pukhraj (39 mg/100 g FW), followed by Kufri Jyoti (36 mg/100 g FW) and Kufri Chipsona-1 (25 mg/100 g FW), and the same trend occurred during storage (Fig. 4). Cultivar differences in phenol content were reported earlier (Kumar 2011; Kumar et al. 2012). Phenol content increased non-significantly at 90 DOS whereas increase in total

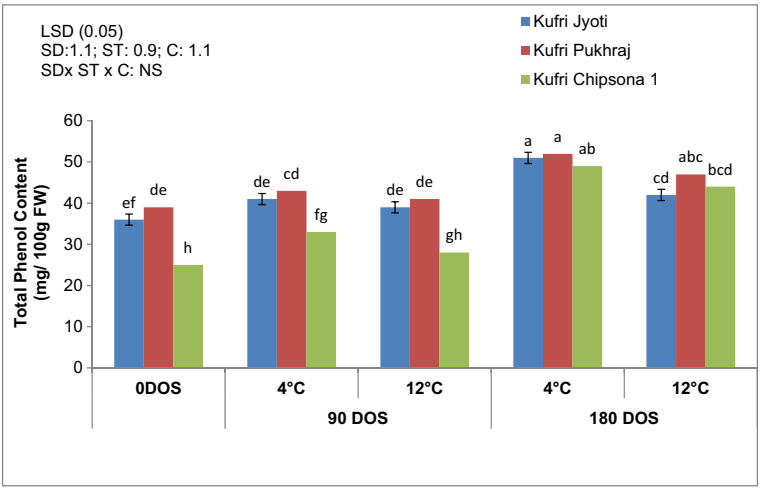

Fig. 4 Changes in total phenol content (mg/100 g fresh weight) in the three potato cultivars during low-temperature storage [Mean separation has been done using Tukey's test. Different letters indicate significant differences between cultivars ($P < 0.05$). Standard error bars represent standard error of interaction between storage duration, temperature and cultivar] (*SD* storage duration, *ST* storage temperature, *C* cultivar, *DOS* days of storage)

phenol was significant after 180 DOS in all the cultivars. Total phenol content was higher at 4 °C as compared to 12 °C in all the three cultivars. Low-temperature storage in potato has been shown to induce generation of phenolic compounds via the phenylpropanoid pathway (Dixon and Paiva 1995) due to activation of phenylalanine ammonia-lyase, a key regulatory enzyme in the biosynthesis of polyphenols and de novo synthesis of secondary metabolites (Lewis et al. 1999). The higher phenol content in Kufri Pukhraj did not seem to have a positive effect on storability and processing quality of tubers in this study, although a contribution of total phenols to total antioxidant activity of 58 to 82% has been reported in potato cultivars (Reddivari et al. 2007).

Before storage, catalase activity was highest in Kufri Chipsona-1 (0.078 μmoles/min/g FW), followed by Kufri Jyoti (0.035 μmoles/min/g FW) and Kufri Pukhraj (0.032 μmoles/min/g FW), and a similar trend was recorded in the three cultivars during storage (Fig. 5). Catalase activity increased significantly with the duration of storage up to 180 days in all the three cultivars with a higher increase recorded at 4 °C. Catalase activity at 4 °C was 0.275, 0.262 and 0.217 μmoles/min/g FW after 90 DOS and 0.438, 0.443 and 0.373 μmoles/min/g FW after 180 DOS in Kufri Chipsona-1, Kufri Jyoti and Kufri Pukhraj, respectively. During oxidative stress (ageing and low-temperature storage), catalase activity is reported to increase manifolds. This is probably due to the activation of defence mechanism. Increase in catalase activity leads to more scavenging of reactive oxygen species and therefore protecting cells from damage due to these species (Spychalla and Desborough 1990b; Dipierro and Leonardis 1997; Mizuno et al. 1998; Delaplace et al. 2009).

Peroxidase activity followed the same trend as catalase activity with Kufri Chipsona-1 recording the highest activity (0.754 μmoles/min/g FW) and Kufri Pukhraj showing the lowest activity (0.093 μmoles/min/g FW) before storage as well as after storage (Fig. 6). Before storage, the peroxidase activity differed non-significantly among the three cultivars. Storage up to 90 days increased the activity in all the three cultivars at

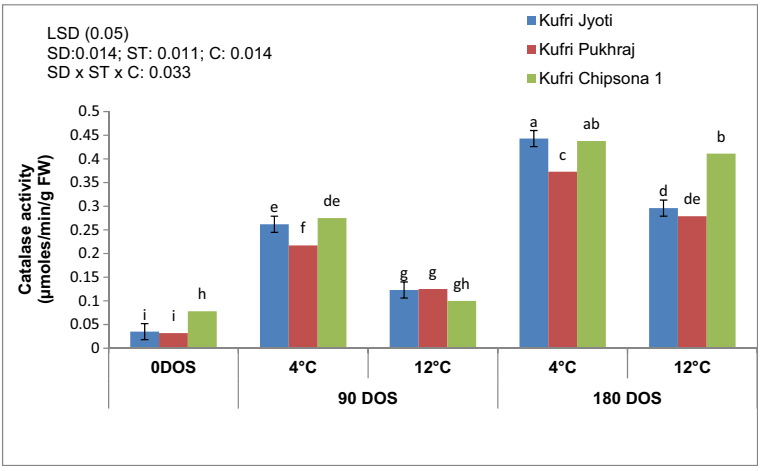

Fig. 5 Changes in catalase activity (μmoles/min/g fresh weight) in the three potato cultivars during low-temperature storage [Mean separation has been done using Tukey's test. Different letters indicate significant differences between cultivars ($P < 0.05$). Standard error bars represent standard error of interaction between storage duration, temperature and cultivar] (*SD* storage duration, *ST* storage temperature, *C* cultivar, *DOS* days of storage)

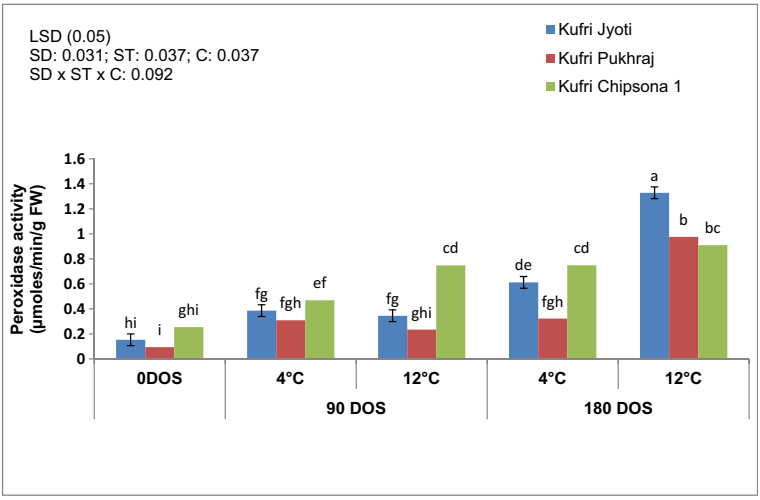

Fig. 6 Changes in peroxidase activity (µmoles/min/g fresh weight) in the three potato cultivars during low-temperature storage [Mean separation has been done using Tukey's test. Different letters indicate significant differences between cultivars ($P < 0.05$). Standard error bars represent standard error of interaction between storage duration, temperature and cultivar] (*SD* storage duration, *ST* storage temperature, *C* cultivar, *DOS* days of storage)

both the storage temperatures. Differences in peroxidase activity between Kufri Jyoti and Kufri Pukhraj were non-significant at 90 DOS. Peroxidase activity was high at 4 °C as compared to 12 °C in Kufri Pukhraj and Kufri Jyoti at 90 DOS, whereas higher enzyme activity was observed at 12 °C in all the tested cultivars after 180 DOS. Cultivars Kufri Jyoti and Kufri Chipsona-1 showed a significant increase in peroxidase activity after 180 DOS at both storage temperatures. Increases in catalase and peroxidase activity indicate an increased rate of activated oxygen production (Spychalla and Desborough 1990b). Both catalase and peroxidase breakdown hydrogen peroxide to water and oxygen and prevent the further formation of free radicals.

Enzyme activity is supposed to be high at low temperatures (4 °C) compared to high temperatures (12 °C) due to a high percentage of dissolved oxygen at low temperature compared to high temperature. The concentration of dissolved oxygen is important because the electron transport chain leaks electrons to oxygen, forming superoxide radicals. However, this is not true for all enzymes. There are several enzymes which are not related to activated oxygen metabolism and during storage, their activities either remain unchanged or show an irregular pattern. Therefore, a general increase of potato tuber enzyme activities would not be expected to accompany the increased superoxide dismutase and catalase activities during low-temperature potato storage (Spychalla and Desborough 1990b).

The level of antioxidants in potato tubers is inversely proportional to sugar accumulation during low-temperature sweetening and cultivars behave differently under different storage conditions. The level of enzymatic antioxidants was cultivar dependent and cultivars with high antioxidative potential possessed good storability with low sugars. Ageing as well as low-temperature storage increased the activity of antioxidative enzymes catalase and peroxidase to detoxify hydrogen peroxide—a product of lipid peroxidation.

The study has shown that both low-temperature and prolonged storage are stress-like situations to potato tubers leading to lipid peroxidation and starch hydrolysis. Cultivar Kufri Chipsona-1, having higher antioxidant enzyme activity (catalase and peroxidase) and lower lipid peroxidation (in terms of MDA and sugar accumulation), maintains the best chip colour of the three cultivars studied throughout storage (data not included). These features make this cultivar superior for processing purposes. In contrast, Kufri Pukhraj (a table cultivar) has a lower enzymatic antioxidant potential, a higher level of sugar accumulation and more lipid peroxidation, and hence is more susceptible to activated oxygen damage.

Conclusion

The following recommendations can be made based on the changes occurring in the contents of sugars and enzyme activities that affect tuber quality, in the three popular cultivars (Kufri Jyoti, Kufri Pukhraj and Kufri Chipsona-1) at two temperatures (4 and 12 °C) under which all long-term storage of potatoes is done in India. Of the two storage temperatures, 12 °C is better than 4 °C for storing ware/processing potatoes due to less accumulation of sugars and a low level of lipid peroxidation resulting in better quality tubers after prolonged storage. Hence, we recommend potato growers and traders to store potatoes meant for ware and processing at 12 °C instead of 4 °C temperature. Cultivar Kufri Chipsona-1 had superior processing characteristics out of storage, and also had the highest levels of catalase and peroxidase and the lowest malondialdehyde content during storage. Cultivar Kufri Chipsona-1 is the most suitable one for long-term storage, whereas cultivar Kufri Pukhraj is the least suitable.

Compliance with Ethical Standards This article does not contain any studies with human or animal subjects.

Conflict of Interest The authors declare that they have no conflict of interest.

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