Effects of γ Irradiation and Storage Temperature on Lipoxygenase Activity and Carotenoid Disappearance in Potato Tubers (*Solanum tuberosum* L.)

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With the aim of exploring the causes for the enhanced destruction of carotenoids in irradiated potato tubers during storage at 15 °C, changes in carotenoids and lipoxygenase activity of irradiated and nonirradiated tubers (cv. *Kufri chandramukhi*) were compared during 6 months of storage at 4, 15, 20, and 25–30 °C (ambient temperature). Carotenoid content tended to decrease in potatoes stored at 15 and 20 °C, while at 4 and 25–30 °C it increased with advancing storage. Irradiation enhanced the carotenoid disappearance in potatoes stored at 15 and 20 °C and reduced its formation at 4 and 25–30 °C. Irradiation at a sprout-inhibiting dose of 100 Gy caused an immediate decline in lipoxygenase activity and also its capacity for cooxidation of β-carotene. The reduced lipoxygenase activity of irradiated potatoes was seen throughout storage regardless of the storage temperature. Irradiated tubers showed decreased protein content and increased levels of peptides and amino acids. No interrelationship seems to exist between lipoxygenase activity and destruction of carotenoids in irradiated potato tubers.

γ irradiation at low dosages of 75–150 Gy for sprout inhibition combined with storage at 10 or 15 °C has been suggested as an alternative technology for the long-term storage of market potatoes in the tropics in lieu of the conventional cold storage at 2–4 °C (Thomas et al., 1978). However, extended storage of potatoes at 10 or 15 °C was found to result in a decrease in the concentration of carotenoid pigments present initially; irradiation further enhanced the disappearance of carotenoids during storage at these temperatures (Thomas and Joshi, 1977; Janave and Thomas, 1979). Carotenoids impart the characteristics creamish or pale yellowish color to the potato tuber flesh. It was therefore of interest to study the probable causes for the enhanced loss of carotenoid pigments observed in irradiated potatoes during storage.

The enzyme lipoxygenase (linoleate:oxygen oxidoreductase EC 1.13.11.12) catalyzes the oxygenation of the *cis,cis*-1,4-pentadiene moiety in polyunsaturated fatty acids such as linoleic and linolenic acids and forms 9- or 13-hydroperoxides of these fatty acids (Adams and Ongley, 1989; Sekiya et al., 1977). The hydroperoxides possessing powerful oxidizing action are believed to be involved in the secondary reactions leading to the loss of characteristics color of some food products as a result of the cooxidation of pigments (Eskin et al., 1977). The role of lipoxygenase in the bleaching of carotenoids in alfalfa was suggested by Michell and Hauge (1946), and its association with the destruction of carotenoids was first reported by Sumner (1943).

The present study was undertaken to examine the possible role of lipoxygenase in the destruction of carotenoids occurring in potato tubers during storage and how irradiation affects the enzyme activity.

EXPERIMENTAL PROCEDURES

Tubers of the cultivar *Kufri chandramukhi* were irradiated within 1 month of harvest to a dose of 100 Gy in a ^{60}Co package irradiator (AECL) in air at 25–30 °C. The dose rate was approximately 17 Gy/min. Nonirradiated tubers served as control. Irradiated and control tubers, 20 kg each, were stored in ventilated plastic crates at ambient temperature (25–30 °C, RH 55–75%) and at 20, 15, and 2–4 °C (RH 80–85%). At monthly intervals duplicate samples of five potato tubers each, from both control and irradiated lots, were removed from the respective storage temperatures and used for the various analyses. Peeled tubers were cut into small pieces, mixed thoroughly at ice temperature, and used immediately for the different analyses.

Linoleic acid (Fluka) and oleic acid (Koch-Light Laboratories Ltd., London) were used as substrates for determining lipoxygenase (LOX) activity. Tween 80 (polyoxyethylene sorbitan monooleate), Tween 20 (polyoxyethylene sorbitan monolaurate), Triton X-100 (*p*-isooctylphenoxyethoxyethanol), and β-carotene (Type II from carrots) were from Sigma Chemical Co. (St. Louis, MO). All other chemicals and solvents used were of analytical grade. Solvents were distilled prior to use.

Total Carotenoids. Carotenoids were extracted from 20 g of tissues in duplicate with a cold acetone: *n*-hexane mixture (75:60 v/v) until the filtrates were colorless. The pooled filtrate was freed of acetone by repeated washing with distilled water, and the hexane layer containing carotenoids was dried over anhydrous sodium sulfate. The absorbance at 450 nm was measured in a Varian DMS 100 spectrophotometer. The amounts present were calculated with reference to a standard graph made for β-carotene (Thomas and Joshi, 1977).

Extraction and Assay of Lipoxygenase Activity. Twenty grams of flesh tissue was homogenized under ice condition in a Sorvall omnimixer at a speed setting of 3 for 3 min with 20 mL of extracting media containing 0.25 M sodium phosphate buffer, pH 6, 1% Triton X-100 and 10^{-2} M sodium metabisulfite ($Na_2S_2O_5$). The homogenate was centrifuged at 12000*g* for 20 min, in a Sorvall RC-2 refrigerated centrifuge. The pellet was resuspended in 20 mL of extracting media containing 10^{-4} M $Na_2S_2O_5$, homogenized, and centrifuged as above. The two supernatants were pooled and kept in ice for measurement of lipoxygenase activity, proteins, peptides, and amino acids.

Lipoxygenase was assayed polarographically by using a Clark oxygen electrode and linoleic acid as substrate (Grossman and Zakut, 1979; Feys et al., 1980). Substrate was prepared by diluting a mixture of linoleic acid (0.1 mL), Tween 20 (0.15 mL), and 0.1 N NaOH (10 mL) to a total volume of 50 mL with dis-

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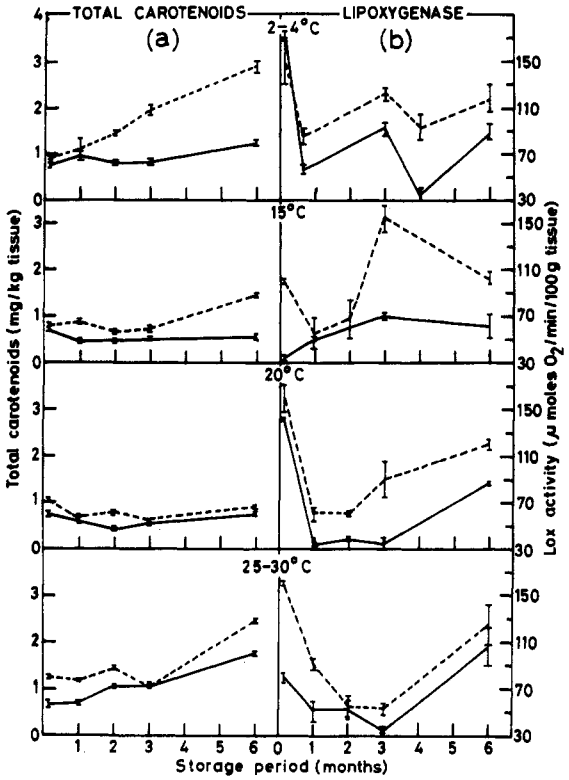

Figure 1. Profiles of total carotenoids and lipoxygenase in control and irradiated potatoes on storage at four different temperatures. Each point represents mean ± SD of six determinations from duplicate extracts from five tubers each from control (- - -) and 100-Gy irradiated (—) potatoes.

tilled water. The reaction system of 3 mL contained air saturated 0.2 M sodium phosphate buffer of pH 6, 0.3 mL of 6.6 mM linoleic acid, and 0.1 mL of enzyme preparation. Enzyme activities were calculated from initial rates of oxygen uptake. The enzyme activity was further confirmed spectrophotometrically from the increase in absorbance at 234 nm. No activity could be detected by either method (polarography and spectrophotometry) when either oleic acid was used as substrate or enzyme preparation was heat inactivated in a boiling water bath for 15 min.

Cooxidation of β-Carotene. The carotene bleaching activity of lipoxygenase was measured according to the method of Ben-Aziz et al. (1971). An optically clear aqueous solution of β-carotene was prepared as follows. The required quantity of β-carotene was initially dissolved in a small volume of chloroform to which Tween 80 was added. After mixing, the chloroform was evaporated off by passing nitrogen gas, and the mixture was dissolved in 0.2 M citrate phosphate buffer, pH 6, containing EDTA (0.25%). The reaction system contained 2.8 mL of aqueous β-carotene (10 μM) preparation having 0.1% Tween 80, 0.6 mL of linoleic acid (10 mM), and 0.1 mL of enzyme preparation. The enzyme solution was added at zero time, and the initial rate of decrease in absorbance was recorded in a Varian double-beam spectrophotometer at 455 nm.

Proteins, Peptides and Amino Acids. Soluble protein content in the supernatant of the centrifuged buffer extract was determined according to the method of Lowry et al. (1951). Proteins in the buffer extracts were precipitated by addition of 10% TCA, and after centrifugation, the peptides and amino acids present in the supernatant were measured as tyrosine equivalents by the Miller (1959) method.

RESULTS

The changes occurring in total carotenoids content and lipoxygenase activity of irradiated and control potatoes during 6 months of storage at 4, 15, 20, and 25–30 °C (room temperature) are shown in Figure 1. Tubers stored at 15 and 20 °C always showed comparatively lower levels of carotenoids than those stored at either 4 or 25–30 °C. At the latter temperatures the carotenoid concentration increased with advancing storage, whereas at 15 and 20 °C the carotenoid levels showed a decreasing trend during the first 3 months and thereafter either remained constant or increased slightly. Irrespective of the temperature of storage, irradiated tubers always recorded lower carotenoid content than nonirradiated tubers (Figure 1a).

Lipoxygenase activity in both control and irradiated potatoes generally showed a decrease at all storage temperatures in the first month and slightly fluctuating levels during the subsequent 2 months followed by a rise in activity at 6 months, the exception being the trend observed in irradiated tubers at 15 °C, which showed low initial activity followed by a gradual rise during storage (Figure 1b).

A comparison of the lipoxygenase activity in irradiated and control potatoes clearly indicates a decline in enzyme activity following irradiation which presisted at all temperatures during the entire storage period of 6 months. The percent decrease in carotenoid levels and lipoxygenase activity in irradiated potatoes stored for 6 months as compared to control tubers is shown in Table I. Maximum decrease in carotenoid content and lipoxygenase activity was noted in irradiated tubers stored at 15 °C.

Figure 2 gives data on the lipoxygenase activity in potatoes irradiated to doses of 50, 100, 150, and 200 Gy. A dose-dependent decrease in enzyme activity was noted immediately after irradiation, and the same trend was discernible in tubers even after a month of storage at room temperature. Also, 99% of the total activity could be extracted from both control and irradiated tubers with extraction media devoid of Triton X-100 (data not shown), which indicated that the enzyme was present in the soluble form.

The cooxidation of β-carotene by potato lipoxygenase is shown in Figure 3. The enzyme from irradiated potatoes exhibited a reduced rate of cooxidation of β-carotene as compared to enzyme from control tubers. The data show that irradiation not only affected the enzyme activity per se but also resulted in a lowering of its capacity for cooxidation of β-carotene.

Addition of β-carotene at different concentrations ranging from 0.17 to 33 μM levels in the reaction mixture inhibited potato lipoxygenase activity as assessed by the rate of oxidation of linoleic acid (Table II). However, the magnitude of inhibition of linoleic acid oxidation by β-carotene was higher with enzyme preparations from control potatoes as compared to irradiated tubers. Thus, at 3.33 μM β-carotene the inhibition in lipoxygenase activity was 51% in control against only 18% in irradiated samples.

The enzyme from both irradiated and control potatoes showed a pH optima in the range 5–6.

Table III shows data for soluble protein content of irradiated and control tubers as a function of storage period at different temperatures. Generally speaking, irradiated potatoes recorded lower protein values, and this was accommodated by increased levels of peptides and amino acids (Table IV). These differences were statistically significant ($p \leq 0.05$) in over 80% of the esimations. Similar results were obtained with another cultivar, *K. lalima*, under identical conditions of storage (results not shown).

DISCUSSION

Lipoxygenase from different foodstuffs of plant origin such as soybean (Ikediobi and Snyder, 1977; Grosch and

Table I. Lipoxygenase and Total Carotenoid Levels in *K. chandramukhi* Potatoes Subjected to Irradiation (100 Gy) and Storage for 6 Months

temp of storage, °C	lipoxygenase activity, μmol of O_2 min^{-1} (100 g of tissue)$^{-1}$		% decrease in irradiated tubers	total carotenoids, mg/kg of tissue		% decrease in irradiated tubers
	control	irradiated		control	irradiated	
2–4	111.18 ± 11.52	89.16 ± 6.62	24.55	2.86 ± 0.16	1.23 ± 0.01	56.99
15	103.62 ± 4.91	62.57 ± 10.55	39.62	1.45 ± 0.06	0.51 ± 0.04	64.82
20	120.36 ± 3.00	86.40 ± 0.36	28.20	0.93 ± 0.02	0.78 ± 0.03	16.13
25–30	126.35 ± 16.42	106.01 ± 17.83	16.10	2.48 ± 0.07	1.75 ± 0.01	29.44

[a] Values are mean ± SD of six determinations.

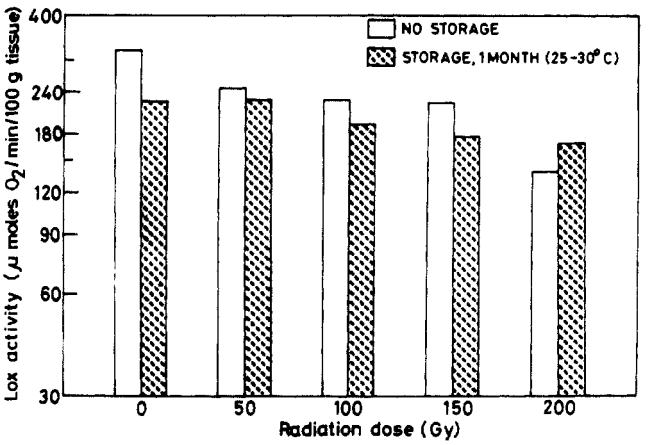

Figure 2. Dose-dependent loss in lipoxygenase activity in potatoes following irradiation and storage. Potatoes exposed to 50-, 100-, 150-, and 200-Gy γ radiation doses were assayed for enzyme activity immediately after irradiation as well as after 1 month of storage at ambient temperature (25–30 °C).

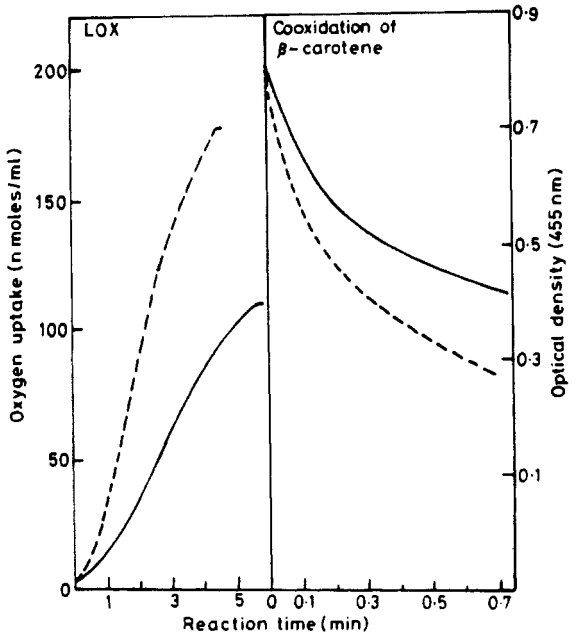

Figure 3. Lipoxygenase and cooxidation of β-carotene activities in control and irradiated tubers following storage at 15 °C for 3 months. Lipoxygenase activity and cooxidation of β-carotene were measured as described in the text from control (- - -) and 100-Gy irradiated (—) potatoes. The carotene bleaching activity in control and irradiated samples was calculated to be 1288 and 1096 units/100 g fresh weight, respectively, suggesting 14.9% loss.

Laskawy, 1979; Barimalaa and Gordon, 1988), peas (Arens et al., 1973), and bean and potatoes (Grosch et al., 1976) is known to cooxidize carotenes with high velocity. However, most studies on the carotene bleaching activity of lipoxygenase are based on the capacity of the enzyme to cooxidize carotenes added to the reaction mixture. To our knowledge there appears to be no report in the literature relating carotenoid loss and lipoxygenase activity in storage organs.

Table II. Effect of β-Carotene Addition on Lipoxygenase Activity

enzyme source	concn of added β-carotene, μM	lipoxygenase, μmol of O_2 min^{-1} (100 g of tissue)$^{-1}$	inhibition, %
control	nil	27.70	nil
	0.17	17.81	35.70
	0.70	18.42	33.50
	3.33	13.52	51.19
	10.00	20.19	27.11
	33.33	23.75	14.26
irradiated	nil	6.93	nil
	3.33	5.69	17.89
	10.00	7.17	nil

[a] The values are the average of two determinations. Enzyme activities were determined polorgraphically as described in the text.

The results of the present study do not indicate an interrelationship between the activity of the enzyme and the disappearance of carotenoids observed in potato tubers stored at 15 or 20 °C, particularly after irradiation. If the enhanced carotenoid destruction observed in irradiated potatoes was associated with lipoxygenase, an increase in enzyme activity can be expected following irradiation. On the contrary, irradiated potatoes irrespective of the duration or temperature of storage always recorded lower levels of lipoxygenase activity as compared to control tubers, which does not suggest a role for this enzyme in the destruction of carotenoids in situ. Heme proteins such as cytochrome *c* and peroxidase are also known to act as potent catalysts in the oxidation of carotene (Blain et al., 1968; Blain 1970; Ben-Aziz et al., 1971). In red pepper fruits the presence of a carotene-oxidizing fraction which exhibited properties similar to those of a peroxidase has been reported (Kanner et al., 1977). It is likely, therefore, that enzyme other than lipoxygenase, possibly peroxidase, may have some role in the destruction of carotenoids in potatoes. Alternatively, direct oxidation of carotenoids (Chichester and Nakayama, 1965) or that mediated by ascorbic acid (Kanner and Mendel, 1976) may also be involved. Such suggestions, however, need verification.

Available evidence seems to suggest that lipoxygenase may not be involved in the destruction of carotenoids in intact plant organs and tissues. In tomato fruits lipoxygenase activity was found to increase proportionally to the progressive development in ripening from mature green to mature red stages (Daood and Biacs, 1988). Our results also point to a similar increase in lipoxygenase activity associated with the increase in carotenoid concentration in potato tubers toward the latter part of storage. It has been reported that in developing buds and leaves of apricot, apple, and liliac lipoxygenase activity and carotene content increased during the early phases of vegetative bud development but during the period of active development

Table III. Protein Levels in Irradiated (100 Gy) and Control *K. chandramukhi* Potatoes during Storage at Different Temperatures

temp of storage, °C	treatment	protein content[a] after a storage period of 3 days	30 days	60 days	90 days	180 days
2–4	control	1.058 ± 0.016	1.000 ± 0.079	1.165 ± 0.031	1.100 ± 0.140	0.967 ± 0.072
	irradiated	1.188 ± 0.017	0.960 ± 0.080[a]	1.151 ± 0.061[a]	1.00 ± 0.013[a]	0.947 ± 0.448[a]
15	control	1.131 ± 0.023	0.957 ± 0.010	0.998 ± 0.128	1.063 ± 0.046	1.155 ± 0.098
	irradiated	0.764 ± 0.008	0.728 ± 0.053	0.806 ± 0.033	1.120 ± 0.020[a]	0.688 ± 0.197
20	control	1.130 ± 0.078	0.868 ± 0.003	0.919 ± 0.023	1.080 ± 0.010	0.780 ± 0.079
	irradiated	0.974 ± 0.070	0.870 ± 0.011[a]	0.770 ± 0.015	0.860 ± 0.040	0.707 ± 0.135[a]
25–30	control	1.124 ± 0.005	0.811 ± 0.015	0.925 ± 0.020	0.840 ± 0.020	0.972 ± 0.052
	irradiated	1.100 ± 0.009	0.700 ± 0.049	0.755 ± 0.040	0.766 ± 0.025	0.662 ± 0.078

[a] Expressed as grams per 100 grams of fresh tubers. Values are mean ± SD of five determinations. As compared to control, the difference in values of irradiated samples is statistically significant ($p \leq 0.05$) except those marked with superscript a.

Table IV. Changes in Peptide and Amino Acid Levels in Control and Irradiated (100 Gy) *K. chandramukhi* Potatoes during Storage at Various Temperatures

temp of storage, °C	treatment	peptides and amino acids content[a] after a storage period of 3 days	30 days	60 days	90 days	180 days
2–4	control	459.80 ± 3.96	403.55 ± 38.80	360.48 ± 14.76	331.00 ± 15.23	660.20 ± 94.32
	irradiated	464.40 ± 7.61[a]	486.67 ± 113.28[a]	393.80 ± 41.47[a]	490.27 ± 7.79	848.25 ± 61.99
15	control	409.30 ± 22.64	482.80 ± 57.82	343.39 ± 18.74	391.63 ± 11.54	795.50 ± 24.83
	irradiated	519.80 ± 9.90	365.51 ± 8.68[a]	412.88 ± 17.49	370.48 ± 8.24[a]	1024.25 ± 22.34
20	control	524.90 ± 14.14	396.62 ± 31.00	364.95 ± 7.06	382.28 ± 13.93	1083.00 ± 77.36
	irradiated	517.80 ± 4.03[a]	452.20 ± 3.32	427.48 ± 3.12	582.05 ± 13.57	1357.25 ± 28.50
25–30	control	453.60 ± 22.70	393.78 ± 7.43	448.60 ± 20.54	510.95 ± 13.34	1177.30 ± 60.35
	irradiated	459.00 ± 17.40[a]	547.40 ± 4.38	597.08 ± 24.67	604.08 ± 24.26	1347.30 ± 45.32

[a] Expressed as nanomoles of tyrosine equivalents per milligram of protein. Values are mean ± SD of five determinations. As compared to control, the difference in values of irradiated samples is statistically significant ($p \leq 0.05$) except those marked with superscript a.

of young leafy shoots the carotene content increased significantly accompanied by a decline in lipoxygenase activity, with no enzyme activity at all in aging leaves (Lebedev et al., 1978). By use of model systems it was further demonstrated that the oxidative action of lipoxygenase from apple buds increased significantly by addition of low amounts of carotene but at higher concentrations of carotene the enzyme activity decreased. However, our results with potato lipoxygenase indicated that the rate of linoleic acid oxidation was inhibited by carotene even at low concentrations.

The reasons for the decrease in lipoxygenase activity observed in potatoes soon after irradiation and during storage are not known. A lowering of the protein content and increases in peptides and amino acids in irradiated potatoes indicate a possible increase in proteolytic activity. It has been reported that irradiation at sprout-inhibiting dose levels increases proteolytic activity in potato tuber buds tissues (Ussuf and Nair, 1974). It is likely that the decreased lipoxygenase activity in irradiated potatoes may be due to the preferential degradation of the enzyme protein by proteases or changes in the valency state of Fe in the enzyme matrix by γ irradiation. The increased concentrations of carotenoids observed in potato tubers held at 4 and 25–30 °C as compared to those held at 15 and 20 °C suggest that synthesis and accumulation of carotenoids in stored potatoes were temperature dependent. Irradiation at a sprout-inhibiting dose of 100 Gy seems to affect the rate of synthesis and accumulation of carotenoids in stored potatoes as evidenced by the reduced levels of carotenoids recorded even at 4 and 25–30 °C.

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