Changes in Carbohydrates and Enzyme Activities of Sweetpotato Lines during Storage

Yasuhiro Takahata,* Takahiro Noda, and Tetsuo Sato

Crop Quality Laboratory, Department of Crop Breeding, Kyushu National Agricultural Experiment Station, Nishigoshi, Kumamoto 861-11, Japan

Changes in carbohydrates and enzyme activities during storage were studied using four sweetpotato lines. The cultivar Benihayato (BH) showed significantly high levels of sucrose, dextrin, α-amylase, and sucrose synthase (SUS) at the late stage of storage. The starch content of BH was significantly decreased. In contrast, the line Kyukei 123 (Q123) showed a low content of sucrose during storage and its SUS activity was decreased. The starch content and α-amylase activity of Q123 were almost constant during storage. The other two lines showed traits intermediate between those of BH and Q123. The dextrins produced during storage were analyzed by high-performance anion-exchange chromatography and had a close relationship with α-amylase activity in each line. These results showed the key role of α-amylase in starch degradation and the possible role of SUS in sucrose accumulation for varietal differences in carbohydrate changes in sweetpotato roots.

Keywords: *Ipomoea batatas; starch; sucrose; dextrin; α-amylase; sucrose synthase; HPAEC analysis*

INTRODUCTION

Storage of sweetpotatoes induces changes in the carbohydrate fraction of the roots. The carbohydrate composition in sweetpotato roots greatly affects the eating quality and processing traits. Some researchers studied the carbohydrate changes in sweetpotatoes during storage without enzyme analysis (Sistrunk et al., 1954; Picha, 1986, 1987). Sugar concentrations vary with storage conditions and length of storage, depending on the cultivar. In general, the root weight and starch content decrease, while the sucrose content increases. Many researchers have studied the changes in carbohydrates in sweetpotatoes during storage with the idea of determining their basic differences. Walter et al. (1975) studied the relationships among amylolytic enzyme activities, carbohydrate changes and differences in organoleptic properties in baked sweetpotato cultivars during storage. Deobald et al. (1971) reported an increase in glucose, sucrose, or α-amylase for two varieties during a 65-day storage period. In their study, there were no obvious relationships between the patterns of increases in any of the three constituents reported in the data. Baba et al. (1987) also studied the changes in carbohydrates and amylases during storage of the sweetpotato cultivar that lacked β-amylase. Recently, Morrison et al. (1993), using traditional and staple-type sweetpotato lines, reported that the varietal differences in α- and β-amylase activity during storage were significant.

Our preliminary tests also showed the varietal difference in changes in sucrose content during storage over several years of experiments (data not shown). The cultivar Benihayato (BH) greatly increased its sucrose content, and the line Kyukei 123 (Q123) had a relatively low sucrose content and maintained it almost constantly during storage. The cultivar Koganesengan (KS) and the line Kyushu 91 (K91) had intermediate traits between BH and Q123 in sucrose accumulation during storage. The enzymatic basis and a more precise analysis of the carbohydrate changes are needed.

* e-mail: ytaka@ss.knaes.affrc.go.jp

At present, the analysis of the fluctuation in the carbohydrates and their related enzymes in sweetpotatoes during storage, especially for sucrose-metabolizing enzymes and dextrin production, is not sufficiently informative. In the current study, to shed more light on the factors affecting changes in carbohydrates in sweetpotato roots, we studied the relationships among changes in carbohydrates and enzyme activities during storage using four lines.

MATERIALS AND METHODS

Sweetpotato Materials and Storage Conditions. The two cultivars, BH and KS, and the two lines, Q123 and K91, were cultivated in an experimental field under the same conditions at Nishigoshi, Kumamoto, Japan. They were harvested on October 7, 1993, and then stored at 12–16 °C in a semiunderground storage facility. Three roots per each line were sampled for carbohydrates and enzyme analysis at 9, 32, 62, 104, and 138 days after harvest. Only sound roots (150–250 g) were used.

Carbohydrate Analysis. Free sugar contents were determined by 80% EtOH extraction and HPLC according to the method of a previous paper (Takahata et al., 1992). The residue after free sugar extraction was washed with 80% EtOH and centrifuged three times. The precipitate was shaken with 10% EtOH for 4 h to obtain the dextrin fraction (Walter et al., 1975). After centrifuging, aliquots of the supernatant were put into microtubes and evaporated to dryness. The microtubes containing the dextrin fraction were stored under desiccant conditions until analysis. The residue after dextrin extraction was suspended with distilled water and boiled for 2 h to gelatinize the starch. The gelatinized starch was hydrolyzed by amyloglucosidase (Boehringer Mannheim), and the starch content was calculated from the amount of glucose that was determined using the alkaline copper reagent described in the study of Morrison and Karkalas (1990).

The dextrin fraction in microtubes was redissolved with 50 mM sodium acetate buffer (pH 4.9) and incubated with 15 U/mL amyloglucosidase (Boehringer Mannheim) at 55 °C for 2 h. The total dextrin contents were assayed by hexokinase and glucose-6-phosphate dehydrogenase reaction with monitoring of the increase in absorbance at 340 nm (Boehringer Mannheim). High-performance anion-exchange chromatography (HPAEC) was also performed on the dextrin fraction that was prepared separately from that for total dextrin

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Table 1. Saccharides and Enzyme Activities in Four Sweetpotato Lines during Storage

		sucrose[b]			starch[b]			dextrin[b]			α-amylase[c]			SUS[d]			SPS[d]		
	DAH[a]		I[e]	II[f]		I	II		I	II		I	II		I	II		I	II
Koganesengan	9	32.6	a	x	283	a	x	0.129	a	x	0.066	a	xy	8.55	ab	xy	17.91	a	x
	32	37.3	ab	x	295	a	x	0.115	a	x	0.085	a	x	7.00	a	xy	15.70	a	x
	62	33.8	a	x	296	a	x	0.208	ab	x	0.071	a	x	8.35	a	xy	10.11	b	x
	104	36.8	ab	x	285	a	x	0.213	ab	x	0.090	a	x	12.24	b	x	9.67	b	x
	138	40.5	b	x	301	a	x	0.252	b	x	0.117	b	xy	6.66	a	x	9.89	b	xy
Benihayato	9	43.1	a	y	161	a	y	0.402	a	y	0.083	a	x	10.78	a	xz	12.32	ac	y
	32	58.0	b	y	155	a	y	0.951	b	y	0.216	b	y	15.54	a	z	8.65	ab	y
	62	56.8	b	y	154	a	y	1.474	c	y	0.161	ab	y	15.20	a	z	7.80	b	x
	104	63.8	b	y	127	b	y	0.978	b	y	0.243	b	y	27.85	b	y	12.00	ac	y
	138	63.1	b	y	113	b	y	1.121	bc	y	0.431	c	z	22.00	b	y	14.13	c	x
Kyushu 91	9	25.5	ab	x	291	a	x	0.210	a	x	0.062	a	xy	13.41	a	z	16.13	a	xy
	32	22.2	a	z	312	a	x	0.361	b	x	0.082	ab	xz	10.71	a	x	7.76	b	y
	62	24.1	ab	z	310	a	x	0.442	b	x	0.093	b	x	9.48	a	x	9.77	b	x
	104	29.1	b	z	303	a	xz	0.381	b	z	0.138	c	z	12.20	a	x	7.96	b	xz
	138	37.8	c	x	297	a	x	0.404	b	x	0.206	d	x	10.51	a	x	8.85	b	y
Kyukei 123	9	28.0	ab	x	311	a	z	0.113	a	x	0.051	a	y	6.08	a	y	13.25	a	y
	32	25.4	ab	z	298	a	x	0.116	a	x	0.068	b	z	5.08	a	y	9.21	bc	y
	62	24.3	ab	z	313	a	x	0.141	a	x	0.053	a	x	5.21	a	y	7.59	bde	x
	104	23.5	a	z	316	a	z	0.188	b	x	0.085	c	x	1.42	b	z	6.27	d	z
	138	28.7	b	z	315	a	x	0.134	a	x	0.093	bc	y	1.47	b	z	9.13	ce	y

[a] Days after harvest. [b] mg/g, fresh weight basis. [c] IU/g, fresh weight basis. [d] μmol sucrose/g·h^{-1}, fresh weight basis. [e] Statistical differences by storage period. Means followed by the same letter are not significantly different among each stage period within each line ($P < 0.05$). [f] Statistical differences by line. Means followed by the same letter are not significantly different among each line within each storage period ($P < 0.05$).

quantitation. The dextrin fraction was redissolved with distilled water, vortexed, and allow to stand for about 1 h; 1 M NaOH solution was added to a final concentration of 0.2 M. Immediately after adding NaOH solution, we injected the sample solution onto HPAEC. The HPAEC conditions were those of the method of Koizumi et al. (1989) that was described by Noda et al. (1995). Maltotriose, maltotetraose, maltopentaose, maltohexaose, and maltoheptaose (G3–G7) were used as standards. HPAEC analysis was also performed on some representative samples that were hydrolyzed by amyloglucosidase.

Enzyme Assay. All extraction procedures were carried out at 0–4 °C in ice according to the method of Takahata et al. (1994), unless otherwise described. Samples were ground in 50 mM HEPES–NaOH buffer (pH 7.4) containing 12.5% glycerol, 4 mM $MgCl_2$, 10 mM $CaCl_2$, 2 mM EDTA, and 50 mM β-mercaptoethanol using a homogenizer and were centrifuged at 15000*g* for 10 min. Some portions of the supernatant were directly used for α-amylase assay. The remaining supernatant was dialyzed with 10 mM HEPES–NaOH buffer (pH 7.4) containing 1 mM β-mercaptoethanol. Sucrose synthase (SUS) and sucrose phosphate synthase (SPS) were assayed according to the modification of Hubburd et al. (1989). The assays were performed with a final reaction volume of 70 μL. A 20 μL sample of dialyzed enzyme solution was incubated with 50 mM HEPES–NaOH (pH 7.4), 16 mM $MgCl_2$, 8 mM fructose (for SUS) or fructose 6-phosphate (for SPS), and 8 mM UDP-glucose in a water bath (30 °C) for 20 min. The reaction was stopped by the addition of 70 μL of 1 N NaOH solution. The mixture was heated for 10 min in boiling water to destroy remaining fructose or fructose 6-phosphate and cooled; 250 μL of 0.1% resorcinol in 95% EtOH and 750 μL of 30% HCl were added and heated at 80 °C for 8 min, and the absorbance at 520 nm was measured. Data were expressed as micromoles of sucrose produced per hour per gram, fresh basis.

α-Amylase activity was assayed using Sigma amylase (product no. 577) with a slight modification. Blocked *p*-nitrophenol-linked maltoheptaoses (BPNPG7) were the most suitable substrate for specific α-amylase assay and were confirmed to be applicable for various plant materials (McCleary and Sheehan, 1987; Sirou et al., 1990; Ziegler, 1990). The reaction was carried out with 50 mM MES–NaOH (pH 6.0), 0.8 mM 4,6-ethylidene-G7-PNP, 20 U/mL α-glucosidase, 8 mM $CaCl_2$, 8 mM $MgCl_2$, and 40 mM NaCl; the total volume was 500 μL. The rate of increase in absorbance at 405 nm (30 °C) was determined, and the activities were calculated in international units (IU) as directed by the manufacturer.

RESULTS

Changes in carbohydrate contents are shown in Table 1. The sucrose contents of BH increased sharply at the initial stage and were always highest among the lines during storage. On the other hand, the sucrose content of Q123 was relatively low and hardly changed during storage. KS had an intermediate level of sucrose that did not change greatly during storage; K91 had a low level of sucrose that gradually increased during the late stage of the storage period. The fructose and glucose contents were far less than the sucrose content and changed negligibly during storage in all lines (data not shown). The starch contents of KS, K91, and Q123 were almost constant during storage; however, that of BH decreased during storage.

The total dextrin content of BH was always higher than those of the other three lines. It increased sharply during the initial stage of storage and remained constant in the late period of storage. K91 showed a slight increase in dextrin content at the initial stage, but the content was always lower than 0.5 mg/g (fresh basis) and remained constant in the late period of storage. The total dextrin content of KS and Q123 was far less than that of BH and remained almost constant throughout the storage period.

Figure 1 depicts the chromatograms of HPAEC analysis for a representative sample with and without amyloglucosidase hydrolysis. Almost all peaks detected from 3 up to 7.5 min (peaks 1 and 3–9) were determined to be α-glucan that was composed of an α1–4 and/or an α1–6 bond (maltooligosaccharides), because the peaks disappeared after amyloglucosidase treatment. The profiles of maltooligosaccharide production during storage were different for each line (Figure 2). The cultivar BH obviously had the largest content of maltooligosaccharides at the late stage of storage. In contrast, the maltooligosaccharide contents of KS and Q123 were low

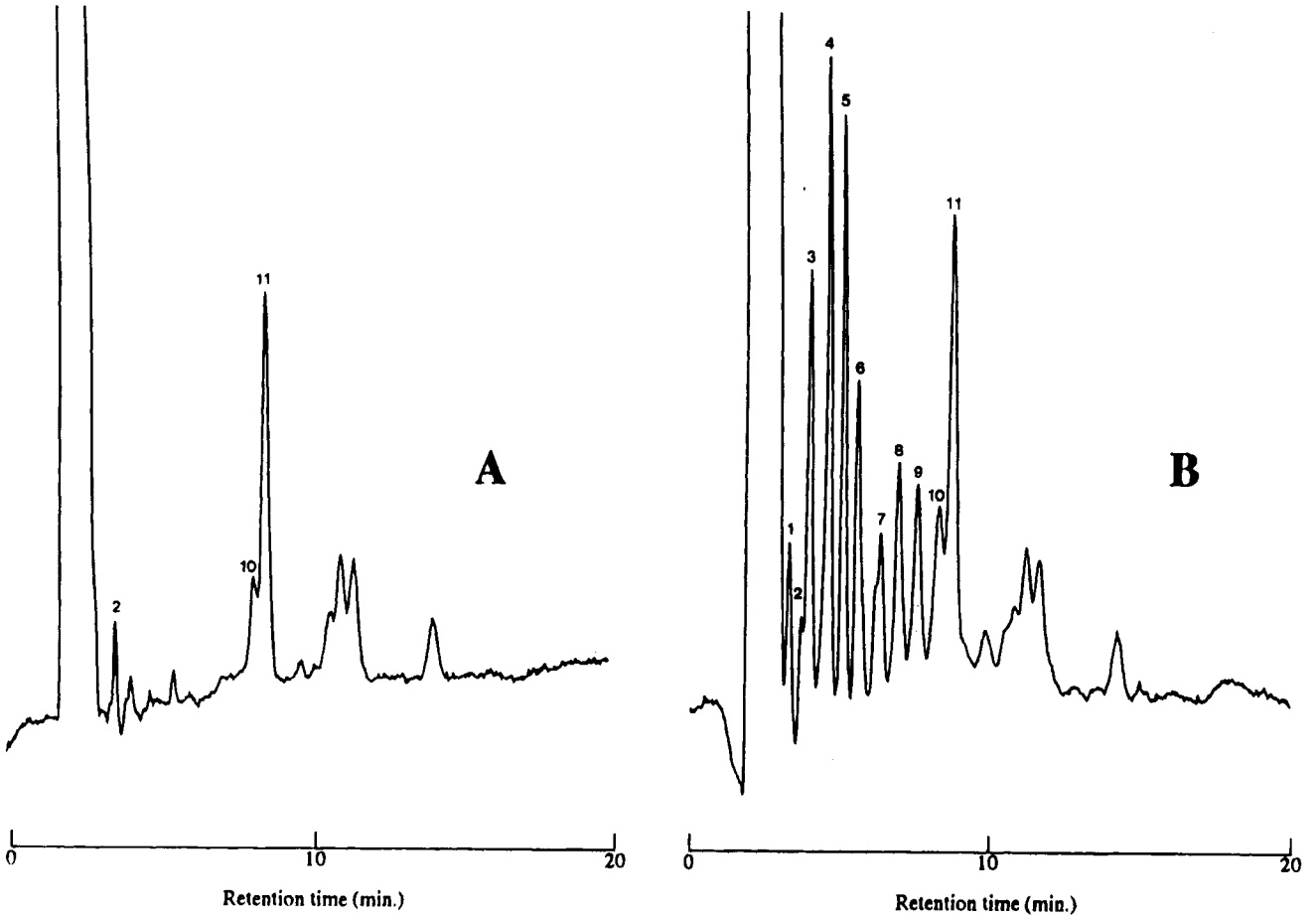

Figure 1. HPAEC chromatograms of dextrin fraction of BH (138 days after harvest) with (A) and without (B) amyloglucosidase hydrolysis. Numerals assigned to each peak correspond to peak numbers in Table 2.

and almost constant during storage. The increase in peak area for each line was approximately proportional to the total dextrin content in Table 1.

Changes in enzyme activities are also shown in Table 1. The activities of α-amylase at the initial stage were similar among all lines; however, BH activity increased during storage and finally reached 4–5 times those of KS or Q123. K91 also significantly increased in α-amylase activity, whereas the rate of increase was gradual compared to that of BH. In contrast, the activities of KS and Q123 were low and showed only slight increase throughout the storage. There was not a clear varietal difference in changes in SPS activity. On the other hand, some features were seen in the changes in SUS activity. The SUS activities were not greatly different among the lines during the early storage period; however, the activity of BH increased during storage. In contrast, the activity of Q123 was always lowest and decreased during storage. The activities of KS and K91 remained constant throughout storage.

DISCUSSION

Walter et al. (1975) reported that the dextrin content of raw sweetpotatoes was less than 0.1 g/100 g of fresh weight; all cultivars had similar amounts, and no increases were noted during storage. They also stated that the relationship between α-amylase activity and dextrin formation appeared to be complex during baking of the roots. In the current study, BH, which had the highest α-amylase activity throughout storage, showed the largest production of dextrin during storage. The total dextrin content of BH at the late stage of storage was 1.0–1.5 mg/g, which exceeded the level reported by Walter et al. (1975). On the other hand, it was thought to be same as the result reported by Walter et al. (1975), that the total dextrin contents of the other three lines were less than 0.5 mg/g (fresh basis). The changes in α-amylase activity also corresponded well to the changes in starch content; i.e., the starch content of BH decreased while the α-amylase activity increased during storage. Many other researchers reported the increase in α-amylase activity and its significant role in decreasing starch during storage or sprouting. Ikemiya and Deobald (1966) showed the increase in α-amylase activity during storage of the Goldrush cultivar. Deobald et al. (1971) also reported that α-amylase increased with storage but had no relationship with the amount of sucrose and glucose. They also mentioned a very large coefficient of variation in α-amylase activities; the data ranged so widely in various shipments that the effects of both curing and varietal differences were overshadowed. Morrison et al. (1993) reported that the α-amylase activity rose from low levels at harvest to a peak level after 90 days of storage. Hagenimana et al. (1994) indicated that the α-amylase activity increased with decreasing starch content during germination and suggested a *de novo* synthesis of the α-amylase. In the current study, BH, which had the largest increase in α-amylase activity among the four lines, showed the largest increase in dextrin content and the largest decrease in starch content during storage.

The precise analysis of the dextrin fraction in sweetpotato roots was very scarce in the past (Walter et al., 1975). The details of dextrin production in raw sweet-

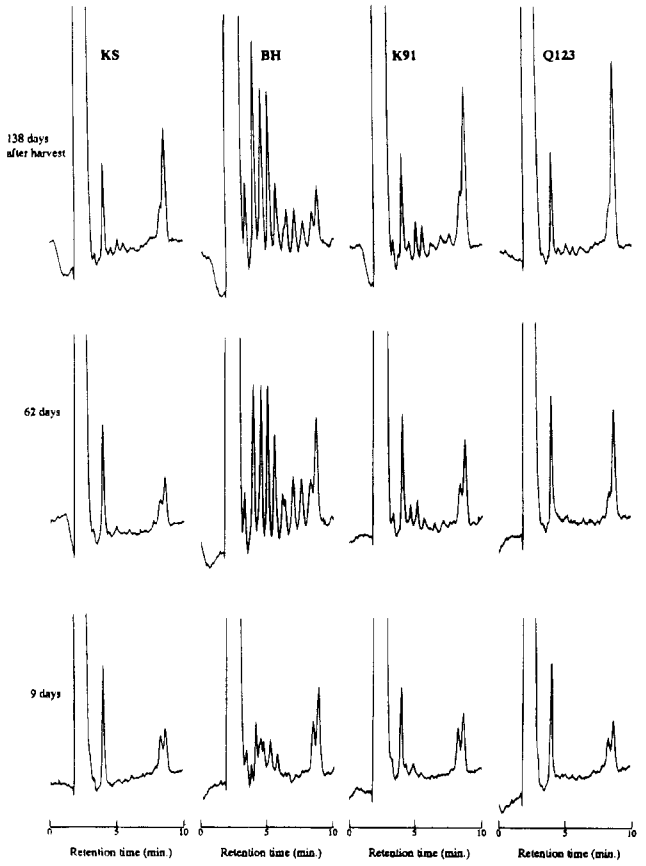

Figure 2. Changes in HPAEC chromatographic profiles of dextrin fraction of each line during storage.

Table 2. Retention Time of Each Peak in Standard (G3–G7) and Sample Solution

name of constituent in standard	retention time in standard[a]	retention time in sample[b]	peak no.[c]
maltotriose (G3)	2.87 (±0.047)		
maltotetraose (G4)	3.24 (±0.066)	3.33 (±0.041)	1
maltopentaose (G5)	3.72 (±0.084)	3.68 (±0.017)	2
		3.96 (±0.052)	3
maltohexaose (G6)	4.28 (±0.094)		
		4.46 (±0.011)	4
maltoheptaose (G7)	4.82 (±0.083)		
		5.03 (±0.047)	5
		5.53 (±0.066)	6
		6.36 (±0.023)	7
		6.96 (±0.011)	8
		7.58 (±0.028)	9
		8.26 (±0.033)	10
		8.69 (±0.013)	11

[a] Average of eight replications (minutes ± standard deviation). [b] Sample BH (138 days after harvest) was used. Average of three replications. [c] Peak numbers correspond to those in Figure 1.

potato roots during storage are still obscure. We analyzed the dextrin fraction more precisely using the HPAEC technique and successfully showed the varietal differences therein (Figures 1 and 2). The peaks that disappeared after amyloglucosidase hydrolysis (peaks 1 and 3–9 in Figure 1) were thought to be the dextrins that had a range of 4–12 degrees of polymerization according to the retention times in previous studies (Koizumi et al., 1989; Noda et al., 1995). However, the retention times of samples in our experiment did not always correspond to those of a standard solution (Table 2). Peak 1 corresponded to maltotetraose, but peaks 3 and 4 did not correspond to any of the standards. This difference in retention times implies the possibility that the dextrins detected by HPAEC in the current study were not always linear chains of α1–4 glucan. α-Amylase plays an important role in hydrolyzing the native starch granules (Beck and Ziegler, 1989); it is an endoamylase that hydrolyzes only the α1–4 bond but not the α1–6 bond. Considering the hydrolysis manner of α-amylase and the HPAEC results in the current study, the dextrins produced during sweetpotato storage were thought to contain isomaltooligosaccharides that were composed of α1–4 and α1–6 bonds. In any event, we clearly showed that α-amylase produced the maltooligosaccharide series, especially in BH, by using the HPAEC technique. On the other hand, we detected peaks that did not disappear after amyloglucosidase hydrolysis (peaks 2, 10, and 11 and all peaks after 11 in Figure 1). Walter et al. (1975) discussed the relationships with dextrin formation and α-amylase activity during baking of the roots. Increasing enzyme activity caused a reduction in the average molecular size of dextrins that was estimated by comparing intrinsic viscosities. However, the enzyme levels were not linearly related to the changes in molecular size. They mentioned that the total dextrin fractions might have contained pectic substances derived from the results of viscosity measurements. Moreover, Takeda et al. (1986), using three cultivars, reported that sweetpotato starches contained 117–139 ppm of organic phosphorus. About two-thirds of the organic phosphorus was attached to the C-6 of the glucose residue and the remainder was attached to C-3. Those phosphate ester groups are a barrier to hydrolysis by α-amylase and amyloglucosidase (Takeda, 1987). According to these previous studies, the peaks that did not disappear after amyloglucosidase digestion in the current study may be a part of the soluble pectic fraction and/or α-glucans bound with phosphorus.

Some researchers studied the sucrose metabolism in sweetpotato roots from various aspects. Invertase and its inhibitor were extensively studied in tissue wounding (Matsushita and Uritani, 1974, 1976, 1977). When the sweetpotato roots suffered γ-irradiation, the sucrose content increased during several weeks after irradiation (Hayashi and Kawashima, 1982a,b). Hayashi et al. (1984) studied the effect of γ-irradiation on the activities of SUS and SPS in sweetpotato roots. They concluded that both of the enzymes played an important role in sucrose accumulation in sweetpotato roots caused by γ-irradiation. Ajlouni and Hamdy (1988) also conducted a similar study and obtained almost the same results. SUS is generally involved in the breakdown of sucrose in plant tissue (Preiss, 1982); however, it was reported to be involved in the synthesis of sucrose in some plant species (Moriguchi and Yamaki, 1988; Moriguchi et al., 1990, 1992). Moreover, Geigenberger and Stitt (1993) recently reported that sucrose synthase catalyzed a readily reversible reaction *in vivo* in potato tubers. In the current study, SUS and SPS were assayed in sweetpotato roots without γ-irradiation during storage. Cultivar BH had a high and increasing sucrose content and showed high SUS activity during storage. In contrast, line Q123 had a low and constant sucrose content and showed relatively low SUS activities that sharply decreased at the late period of storage. Thus, SUS in sweetpotato root may play a significant role in sucrose metabolism during storage. However, SUS in sweetpotato root has been reported to be involved in the breakdown of sucrose instead of the sucrose synthesizing reaction, and the activity sharply decreased im-

mediately after harvest (Murata, 1971a,b). Sucrose metabolism in sweetpotato roots is still not well understood.

Picha (1986) pointed out different sucrose metabolism pathways or enzyme activity deviation with storage between white and orange flesh cultivars. Actually, BH is the only orange flesh cultivar in the current study (Kukimura et al., 1988; Takahata et al., 1993). The changes in α-amylase and SUS activities during storage were apparently different between BH and the other lines. However, it is still obscure that these varietal differences of enzymes are specifically dependent on the difference between orange flesh and others.

The *in vivo* mechanism of converting starch to sucrose in plant sink tissue has not yet been clarified in detail (Beck and Ziegler, 1989). Maeda et al. (1979) reported that the R-enzyme (starch debranching enzyme) had an important role in starch degradation in germinating barley seeds. The cooperative starch hydrolysis by α-amylase and the R-enzyme was most effective. We also investigated the R-enzyme that was assayed with pullulan as the substrate; however, the activity was negligible throughout the storage in each cultivar. On the other hand, Hagenimana et al. (1992) reported that α-amylase was unable to hydrolyze native sweetpotato starch granules in an *in vitro* experiment. They also reported that the role of starch phosphorylase was thought to be vital for the *in vivo* degradation of raw sweetpotato starch during sprouting (Hagenimana et al., 1994). The same mechanism presumably occurred in the current study; however, the role of starch phosphorylase is not the main one in starch degradation because it is unable to attack raw starches and its enzymatic reaction involves exophospholysis. In addition, our results with HPAEC analysis imply the significant role of α-amylase in starch degradation during storage. In conclusion, our results showed the key role of α-amylase in starch degradation and the possible role of SUS in sucrose accumulation for varietal differences in carbohydrate changes in sweetpotato roots. More precise studies on the *in situ* relationship between α-amylase and raw starch and on sucrose metabolism should be done.

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LITERATURE CITED

Ajlouni, S.; Hamdy, M. K. Effect of combined gamma-irradiation and storage on biochemical changes in sweet potato. *J. Food Sci.* **1988**, *53*, 477–481.

Baba, T.; Nakama, H.; Tamaru, Y.; Kono, T. Changes in sugar and starch contents during storage of new type sweetpotato (low β-amylase activity in roots). *J. Jpn. Soc. Food Sci. Technol.* **1987**, *34*, 249–253.

Beck, E.; Ziegler, P. Biosynthesis and degradation of starch in higher plants. *Annu. Rev. Plant Physiol. Plant Mol. Biol.* **1989**, *40*, 95–117.

Deobald, H. J.; Hasling, V. C.; Catalano, E. A. Variability of increase in α-amylase and sugars during storage of Goldrush and Centennial sweetpotatoes. *J. Food Sci.* **1971**, *36*, 413–415.

Geigenberger, P.; Stitt, M. Sucrose synthase catalyses a readily reversible reaction in vivo in developing potato tubers and other plant tissues. *Planta* **1993**, *189*, 329–339.

Hagenimana, V.; Vézina, L. P.; Simard, R. E. Distribution of amylases within sweet potato (*Ipomoea batatas* L.) root tissue. *J. Agric. Food Chem.* **1992**, *40*, 1777–1783.

Hagenimana, V.; Simard, R. E.; Vézina, L. P. Amylolytic activity in germinating sweetpotato (*Ipomoea batatas* L.) roots . *J. Am. Soc. Hortic. Sci.* **1994**, *119*, 313–320.

Hayashi, T.; Kawashima, K. The effect of gamma-irradiation on the sucrose content in sweet potato roots and potato tubers. *Agric. Biol. Chem.* **1982a**, *46*, 1475–1479.

Hayashi, T.; Kawashima, K. Accumulation of sucrose in gamma-irradiated sweet potato roots. *J. Food Sci.* **1982b**, *47*, 2011–2014.

Hayashi, T.; Sugimoto, T.; Kawashima, K. Effect of gamma-irradiation on the activities of sucrose synthase and sucrose phosphate synthase in potato tubers and sweet potato roots. *J. Jpn. Soc. Food Sci. Technol.* **1984**, *31*, 281–284.

Hubbard, N. L.; Huber, S. C.; Pharr, D. M. Sucrose phosphate synthase and acid invertase as determinants of sucrose concentration in developing muskmelon (*Cucumis melo* L.) fruits. *Plant. Physiol.* **1989**, *91*, 1527–1534.

Ikemiya, M.; Deobald, H. J. New characteristic alpha-amylase in sweet potatoes. *J. Agric. Food Chem.* **1966**, *14*, 237–241.

Koizumi, K.; Kubota, Y.; Tanimoto, T.; Okada, Y. High-performance anion-exchange chromatography of homogeneous D-gluco-oligosaccharides and -polysaccharides (polymerization degree ≥50) with pulsed amperometric detection. *J. Chromatogr.* **1989**, *464*, 365–373.

Kukimura, H.; Yoshida, T.; Komaki, K. New sweet potato cultivars, Benihayato and Satsumahikari, making a new turn for processing. *JARQ* **1988**, *22*, 7–13.

Maeda, I.; Jimi, N.; Taniguchi, H.; Nakamura, M. Purification of R-enzyme from malted barley and its role in *in vitro* digestion of barley starch granules. *J. Jpn. Soc. Starch Sci.* **1979**, *26*, 117–127.

Matsushita, K.; Uritani, I. Changes in invertase activity of sweet potato in response to wounding and purification and properties of its invertases. *Plant. Physiol.* **1974**, *54*, 60–66.

Matsushita, K.; Uritani, I. Isolation and characterization of acid invertase inhibitor from sweet potato. *J. Biochem.* **1976**, *79*, 633–639.

Matsushita, K.; Uritani, I. Synthesis and apparent turnover of acid invertase in relation to invertase inhibitor in wounded sweet potato root tissue. *Plant. Physiol.* **1977**, *59*, 879–883.

McCleary, B. V.; Sheehan, H. Measurement of cereal α-amylase: a new assay procedure. *J. Cereal Sci.* **1987**, *6*, 237–251.

Moriguchi, T.; Yamaki, S. Purification and characterization of sucrose synthase from peach (*Prunus persica*) fruit. *Plant Cell Physiol.* **1988**, *29*, 1361–1366.

Moriguchi, T.; Sanada, T.; Yamaki, S. Seasonal fluctuations of some enzymes relating to sucrose and sorbitol metabolism in peach fruit. *J. Am. Soc. Hortic. Sci.* **1990**, *115*, 278–281.

Moriguchi, T.; Abe, K.; Sanada, T.; Yamaki, S. Levels and role of sucrose synthase, sucrose-phosphate synthase, and acid invertase in sucrose accumulation in fruit of Asian pear. *J. Am. Soc. Hortic. Sci.* **1992**, *117*, 274–278.

Morrison, T. A.; Pressey, R.; Kays, S. J. Changes in α- and β-amylase during storage of sweetpotato lines with varying starch hydrolysis potential. *J. Am. Soc. Hortic. Sci.* **1993**, *118*, 236–242.

Morrison, W. R.; Karkalas, J. Starch In *Methods in Plant Biochemistry Volume 2. Carbohydrates*; Dey, P. M., Ed.; Academic Press: London, 1990.

Murata, T. Sucrose synthetase of sweet potato roots Part II. A kinetic study. *Agric. Biol. Chem.* **1971a**, *35*, 1441–1448.

Murata, T. Enzymic mechanism of starch synthesis in sweet potato roots. Part IV. Sucrose synthetase of sweet potato roots (1) Changes in enzyme activity during development and some properties of sucrose synthetase. *J. Agric. Chem. Soc. Jpn.* **1971b**, *45*, 441–448.

Noda, T.; Takahata, Y.; Sato, T. Distributions of the amylopectin chain length of sweet potatoes differing in stages of development, tissue zone and variety. *J. Jpn. Soc. Food Sci. Technol.* **1995**, *42*, 200–206.

Picha, D. H. Sugar content of baked sweetpotatoes from different cultivars and lengths of storage. *J. Food Sci.* **1986**, *51*, 845–846, 848.

Picha, D. H. Carbohydrate changes in sweet potatoes during curing and storage. *J. Am. Soc. Hortic. Sci.* **1987**, *111*, 89–92.

Preiss, J. Regulation of the biosynthesis and degradation of starch. *Annu. Rev. Plant Physiol.* **1982**, *33*, 431–454.

Sirou, Y.; Lecommandeur, D.; Laurière, C. Specific enzymatic microassays of α-amylase and β-amylase in cereals. *J. Agric. Food Chem.* **1990**, *38*, 171–174.

Sistrunk, W. A.; Miller, J. C.; Jones, L. G. Carbohydrate changes during storage and cooking of sweetpotatoes. *Food Technol.* **1954**, *8*, 223–226.

Takahata, Y.; Noda, T.; Nagata, T. Varietal diversity of free sugar composition in storage root of sweetpotato. *Jpn. J. Breed.* **1992**, *42*, 515–521.

Takahata, Y.; Noda, T.; Nagata, T. HPLC determination of β-carotene content of sweet potato cultivars and its relationship with color values. *Jpn. J. Breed.* **1993**, *43*, 421–427.

Takahata, Y.; Noda, T.; Nagata, T. Effect of β-amylase stability and starch gelatinization during heating on varietal differences in maltose content in sweetpotatoes. *J. Agric. Food Chem.* **1994**, *42*, 2564–2569.

Takeda, Y. Actions of various amylases in the vicinity of phosphate groups of potato starch and location of the phosphate groups in the starches. *J. Jpn. Soc. Starch Sci.* **1987**, *34*, 225–233.

Takeda, Y.; Tokunaga, N.; Takeda, C.; Hizukuri, S. Physicochemical properties of sweet potato starches. *Starch / Staerke* **1986**, *38*, 345–350.

Walter, W. M.; Purcell, A. E.; Nelson, A. M. Effects of amylolytic enzymes on "moistness" and carbohydrate changes of baked sweetpotato cultivars. *J. Food Sci.* **1975**, *40*, 793–796.

Ziegler, P. Specific determination of starch hydrolyzing enzyme activities of leaves. *J. Plant Physiol.* **1990**, *136*, 580–586.

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