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ARTICLE

Extensive Variation in Fried Chip Color and Tuber Composition in Cold-Stored Tubers of Wild Potato (*Solanum*) Germplasm

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Cold-induced sweetening and browning in the Maillard reaction have driven extensive research in the areas of plant physiology, biochemistry, and food science in *Solanum tuberosum* because of its importance to the potato-processing industry. Prior research has not characterized wild *Solanum* relatives of potato for tuber composition and has not determined if relationships between tuber composition and chip color after cold storage in wild species are comparable to those found for cultivated potato. Extensive inter- and intraspecific variation for chip color and tuber composition were found in the wild *Solanum* species examined. Tuber sugar profiles suggested that invertase activity at low temperatures differed between and within species. Tuber fructose, glucose, and sucrose concentrations partially explained chip color variation in most accessions, but asparagine concentration and percent dry matter did not. Most wild species had reducing sugar concentrations and chip color scores after 2 °C storage that were less than those in *S. tuberosum* cultivar Snowden. Sugar profiles and relationships between specific sugars and chip color in *Solanum pinnatisectum* were unique among the species examined.

KEYWORDS: Potato; *Solanum* germplasm; extreme cold storage; cold-induced sweetening; low-temperature sweetening; Maillard reaction; tuber sugar concentration; tuber asparagine concentration; chip color; invertase

INTRODUCTION

Free reducing sugars react with amino acids in the Maillard reaction during potato chip production to generate flavor compounds, dark-colored pigments, and acrylamide. Dark-colored chips are undesirable to potato processors, and acrylamide is a known neurotoxin and suspected carcinogen (*1*). Substrates for the Maillard reaction often correlate with chip color (*2*−*6*) and acrylamide content (*7*−*11*) in potato chips. Consequently, limiting substrate concentrations is one way to limit acrylamide formation and mitigate chip darkening (*12*). Fructose, glucose, and sucrose are the most abundant free sugars in cultivated potato tubers (*13*, *14*), and asparagine is the primary amino acid (*12*). Reducing sugar concentration positively correlates with chip color in many potato cultivars (*2*−*6*). The processing industry has used reducing sugar concentrations to predict chip color, and reducing sugar concentrations considered to be acceptable for chip processing have decreased over time from 16.5 to 0.35 mg g^{-1} of dry weight (DW) (**Table 1**) (*15*−*18*). Amino acid composition of potato tubers has not been studied as extensively as sugar composition, but variation in amino acids minimally influenced potato chip color, flavor, and acrylamide production (*9*). Hence, reducing sugar, not asparagine, concentrations are thought to limit the Maillard reaction in *Solanum tuberosum* (*6*). It is not known if this generalization can be extended to tubers from other *Solanum* species.

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Producing light-colored chips consistently is a significant challenge to the potato industry. Over 85% of the annual U.S. potato crop is harvested in the fall, and the shelf life of potato chips is 4−6 weeks. To provide consumers with potato chips year-round, therefore, potato tubers must be stored for up to 10 months. Low-temperature storage is highly beneficial because cold storage temperatures (2−5 °C) extend storage duration by minimizing pathogen activity, reducing water loss, and preventing tuber sprouting. Unfortunately, storage temperatures below 10 °C stimulate cold-induced sweetening (CIS), which is characterized by an accumulation of sucrose and conversion of sucrose to reducing sugars by vacuolar acid invertase (*19*). Tubers for commercial potato chip production are usually stored at 8−10 °C to minimize CIS. Most prior research studies have stored tubers at temperatures as low as 4 °C. Even though long-term potato storage below 4 °C further reduces pathogen activity and premature sprouting, there are few research studies on chip color from tubers stored at 2 °C (*9*, *20*, *21*) because of excessive cold sweetening.

The genetic makeup of potato cultivars influences the extent of CIS (*22*, *23*). Genotypic variation for reducing sugar concentrations and chip color from cold storage exists in potato cultivars (*24*, *25*), but no commercial cultivar consistently meets processing requirements from <8 °C storage. Wild *Solanum* germplasm has been introgressed into many cultivars to improve yield, disease resistance, tolerance of environmental stress, and adaptation to diverse environments. Wild tuber-bearing *Solanum* relatives may contain traits valuable for low-temperature storage,

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but these species have not been evaluated for tuber composition and chip color following cold storage. This study is the first to examine cold-stored tuber composition and the inter-relationships of chip color and tuber sugar and amino acid concentrations in diverse *Solanum* species.

MATERIALS AND METHODS

Plant Materials. Nineteen species that include broad taxonomic and chip color phenotypic diversity after 3−4 months of storage at 1−2 °C were selected from a previous extensive germplasm evaluation (*20*) for detailed analysis. Ten species were represented by multiple plant introductions (PIs) to evaluate intraspecific variation. Additional accessions of *Solanum chacoense* and *S. pinnatisectum* were included in 2006 and 2007 on the basis of observed light chip color and novel sugar profiles, respectively, for these species. PIs with low frequency of botanical seed germination or tuberization and those that did not exhibit light chip color in 2004, 2005, or 2006 were not planted in 2007. *S. tuberosum* cultivar (cv.) Snowden, a variety grown commercially for potato chip production, and four *S. tuberosum* haploid × species hybrids from the USDA Potato Enhancement Laboratory selected for production of potato chips were clonally propagated from tubers and used as controls in 2005, 2006, and 2007 for comparison to the wild species.

Thirty plants per accession were grown in 2004 from botanical seed obtained from the National Research Support Program (NRSP)-6-United States Potato Genebank in Sturgeon Bay, WI. In the following years (2005−2007), tuber seed pieces from the previous year and location were planted when available. If fewer than 30 plants from seed pieces were available for any PI, plants grown from true botanical seed supplemented those grown from seed pieces so that 30 seedlings were produced each year. For each control clone, 8−15 plants were analyzed yearly from each location. All plants were maintained and analyzed individually.

Plant Production. All plant materials were started in greenhouses at Madison or Rhinelander, WI, and transplanted into 10 cm pots with Pro-Mix BX (Premier Horticulture, Inc., Quakertown, PA) potting medium

Table 1. Reducing Sugar Concentrations Used as Thresholds To Predict Chip Color

source	reducing sugar thresholds (mg g^{-1}) FW[a]	DW[b]
Frito-Lay (*15*)	0.07	0.35
Biedermann-Brem *et al.*, 2003 (*16*)	1.00	5.00
Smith, 1987; Dale and MacKay, 1994 (*17*, *18*)	2.0−3.3	10.0−16.5

[a] Converted to reducing sugar concentration from glucose concentration by assuming equal concentrations of glucose and fructose and multiplying by 2. [b] Dry weight converted to fresh weight based on 20% dry matter.

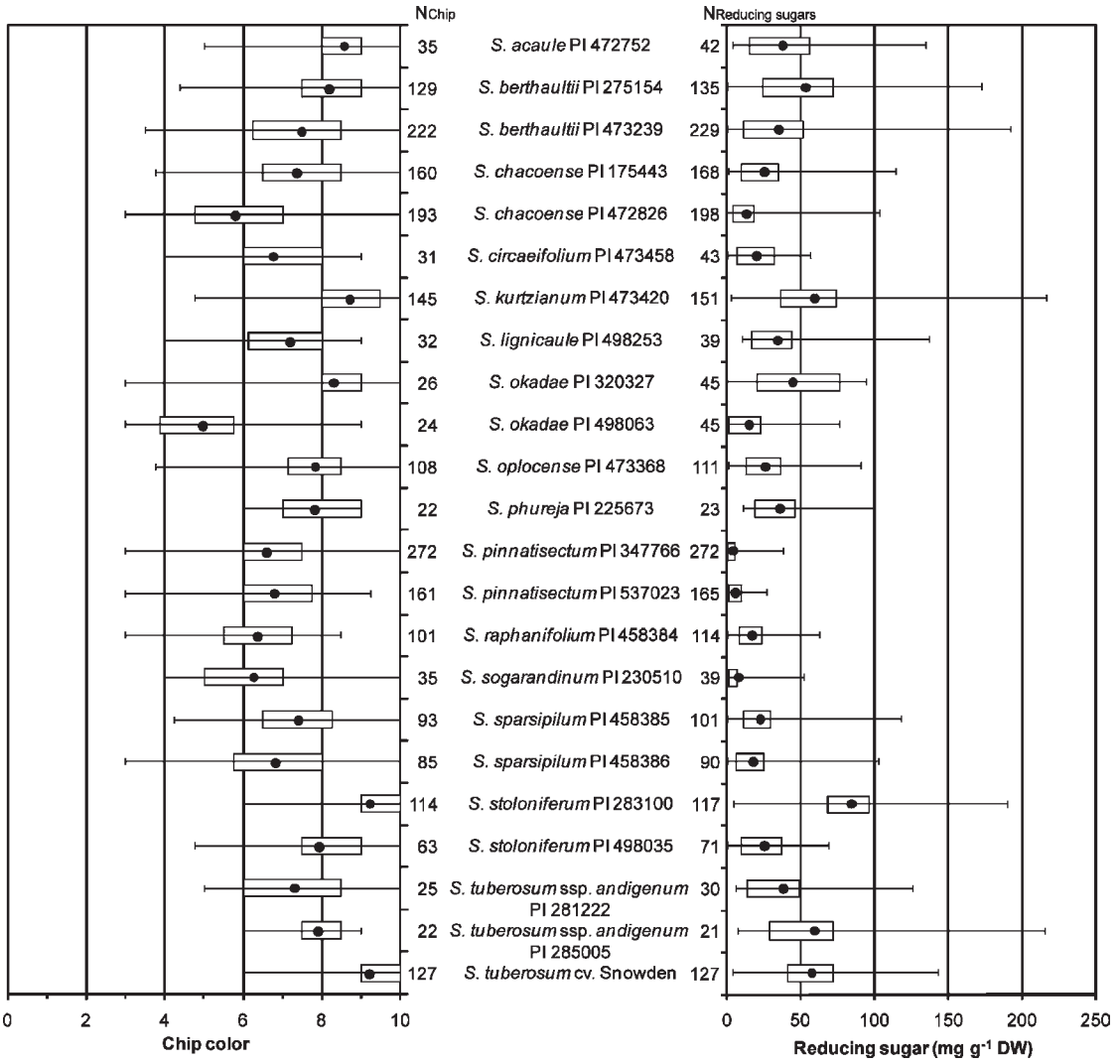

Figure 1. Chip color and reducing sugar concentration (mg g^{-1} of DW) after 3 months of storage at 2 °C varied extensively among and within 23 *Solanum* accessions. *N* = number of plants analyzed. Boxes comprise data from first to third quartiles, accession means are indicated by dots, and whiskers represent maximum and minimum observed values for individual plants. Chip color was scored according to the Potato Chip Institute International Color Chart, where 1 = lightest and 10 = darkest color.

Table 2. Minimum, Maximum, and Mean Values over Four Years and Two Locations for the Variables of Chip Color; Concentrations of Fructose, Glucose, Sucrose, and Asparagine; and Percent Dry Matter

		chip color			fructose (mg g^{-1} of DW)			glucose (mg g^{-1} of DW)			sucrose (mg g^{-1} of DW)			% dry matter			asparagine (μmol g^{-1} of DW)		
species	PI or ID	N[a]	mean	range	N	mean	range	N	mean	range	N	mean	range	N	mean	range	N	mean	range
S. acaule	472752	35	8.6	5−10	42	25	3−89	42	13	0−51	42	74	6−233	30	30	19−39	37	144	38−348
S. berthaultii	275154	129	8.2	4−10	135	23	0−73	135	31	0−103	135	52	8−389	93	22	12−31	74	61	5−305
	473239	222	7.5	4−10	229	19	0−95	229	17	0−98	229	83	1−300	185	22	6−52	80	111	1−499
S. chacoense	175415	46	6.5	3−9	46	5	0−19	46	4	0−13	46	63	28−115	46	31	24−39	b		
	175443	160	7.4	4−10	169	13	1 −56	168	13	0−59	171	33	3−91	143	31	6−44	89	33	7−160
	472826	193	5.8	3−10	199	7	0−34	198	7	0−70	199	43	1−116	170	27	14−42	76	86	1−317
	498320	62	7.5	4−10	61	12	0−77	60	12	1−68	61	66	21−127	62	30	10−57			
	498325	27	8.4	6−10	27	23	0−78	27	25	3−67	27	71	26−137	27	28	18−36			
	537025	47	6.8	4−9	47	8	1−31	47	10	1−29	47	55	2−121	47	30	21 −41			
	568971	52	7.0	4−10	51	9	1−35	51	10	0−51	51	64	27−122	52	30	3−56	6	23	11−35
S. circaeifolium	473458	31	6.8	4−9	43	12	0−33	43	9	0−35	43	27	2−85	17	24	13−30	41	103	8−581
S. iopetalum	498025	2	7.8	8−8	5	20	9−39	5	16	5−27	5	60	28−93	3	21	15−25	4	189	74−247
S. kurtzianum	473420	145	8.7	5−10	151	31	1−114	151	29	2−102	152	22	6−111	126	30	13−44	89	53	5−198
S. lignicaule	498253	32	7.2	4−9	39	19	7−65	39	16	2−72	41	36	6−93	22	20	13−30	30	120	17−304
S. medians	230507	6	5.3	4−8	15	21	3−46	15	16	1−42	15	41	16−74	5	21	18−29	15	148	40−553
	310994	14	4.9	3−7	28	11	0−29	28	7	0−22	28	47	19−120	8	22	19−26	28	160	2−614
S. multiinterruptum	275272	1	8.0	8−8	5	24	1−51	5	29	2−53	5	23	0−33	3	23	22−24	6	84	5−153
	365337	1	5.0	5−5	5	26	2−66	5	15	8−23	5	64	18−133	1	35	35−35	4	176	19−348
S. okadae	320327	26	8.3	3−10	45	24	0−47	45	21	0−49	45	21	0−59	19	33	24−40	43	110	2−802
	498063	24	5.0	3−9	45	8	0−38	46	8	0−39	46	27	0−83	28	28	19−33	44	77	2−296
	498064	36	6.0	4−10	61	9	0−44	61	8	0−46	61	41	4−142	18	26	16−34	52	37	2−344
S. oplocense	473368	108	7.8	4−10	111	11	0−45	111	16	1−56	111	42	8−200	82	27	16−37	59	56	1−560
S. phureja	225673	22	7.9	6−9	26	33	4−48	23	17	3−51	26	57	16−169	13	19	9−22	24	210	2−868
	243465	13	6.6	3−9	15	14	1−35	15	13	2−30	15	53	22−75	9	22	15−27	13	288	6−903
S. pinnatisectum	184774	152	6.7	3−10	153	4	0−31	151	2	0−16	157	137	1−590	122	33	15−49	155	131	2−882
	253214	62	7.5	4−10	62	1	0−2	62	1	0−5	62	158	80−243	62	32	24−43	62	113	3−243
	275231	57	6.5	3−9	57	1	0−2	57	1	0−3	57	137	90−209	57	32	15−39	57	154	56−269
	275233	60	7.3	4−10	61	1	0−2	61	1	0−3	61	152	84−207	61	32	24−46	61	118	10−241
	275235	62	6.8	3−10	62	1	0−8	62	1	0−6	62	157	43−222	61	29	21−44	62	134	5−262
	275236	62	6.2	3−9	62	1	0−9	62	1	0−8	62	151	77−413	62	32	19−44	62	71	6−213
	347766	272	6.6	3−10	273	3	0−25	272	2	0−14	274	118	17−859	248	33	5−56	211	183	0−1213
	537023	161	6.8	3−9	165	5	0−20	165	2	0−8	167	124	1−277	132	33	19−46	158	170	2−989
S. piurae	473501	3	6.2	6−7	7	11	2−27	7	10	2−25	7	69	41−99	4	28	24−34	6	73	24−199
S. raphanifolium	310998	2	5.5	4−7	4	2	0−5	4	2	1−4	4	41	24−57	1	28	28−28	4	51	23−102
	458384	101	6.4	3−9	115	9	0−32	114	8	0−31	115	33	5−70	86	24	14−35	74	145	9−398
	458408	9	6.5	4−8	15	8	1−38	15	5	0−24	14	33	18−64	9	27	19−35	10	141	48−257
	473526	4	5.8	3−10	16	4	0−13	15	3	0−9	18	49	10−110	2	23	21−25	14	104	3−188
S. sogarandinum	230510	35	6.3	4−10	40	4	0−32	39	5	0−23	43	37	2−117	32	25	15−32	32	85	3−276
S. sparsipilum	230502	49	6.7	4−10	61	9	1−45	62	6	0−39	62	93	41−243	39	31	20−48	60	128	6−899
	458385	93	7.4	4−10	102	12	0−49	101	12	0−69	102	64	22−150	70	28	20−36	96	97	1−849
	458386	85	6.9	3−10	90	9	0−56	90	9	0−47	90	56	20−131	67	31	17−40	55	60	4−305
S. stoloniferum	283100	114	9.2	6−10	117	46	3−102	117	38	2−88	117	48	15−346	92	25	18−59	66	78	7−491
	498027	54	8.8	7−10	64	28	0−63	64	22	2−52	64	47	8−198	46	27	17−40	46	129	2−657
	498035	63	8.0	5−10	71	14	1−40	71	11	1−29	70	66	14−135	36	29	22−38	68	126	3−846
S. tuberosum	281222	25	7.4	5−10	30	20	4−66	30	19	2−60	28	47	18−107	14	19	13−24	22	90	4−252

Table 2. Continued

species	PI or ID	chip color			fructose (mg g^{-1} of DW)			glucose (mg g^{-1} of DW)			sucrose (mg g^{-1} of DW)			% dry matter			asparagine (μmol g^{-1} of DW)		
		N^a	mean	range	N	mean	range	N	mean	range	N	mean	range	N	mean	range	N	mean	range
ssp. *andigenum*	285005	22	7.9	6−9	21	27	4−105	21	33	3−110	21	37	18−79	16	22	16−29	20	130	9−578
S. tuberosum	Sebago	5	8.4	8−9	5	21	12−42	5	13	7−21	5	38	31−50	5	18	12−24			
	Snowden	127	9.3	6−10	127	29	2−69	127	29	2−75	127	39	17−138	126	24	4−35	22	110	56−170
S. tuberosum × *S. pinnatisectum*	461	16	6.9	5−9	16	4	0−17	16	5	0−20	16	106	59−144	16	24	20−29			
S. tuberosum × *S. stenotomum*	AH57.8	89	9.0	7−10	90	39	9−169	90	32	5−158	90	46	20−100	90	20	11−26	15	99	16−240
(*S. tuberosum* × *S. chacoense*) × *S. raphanifolium*	GH28.9	82	8.0	3−10	82	20	1−81	82	21	3−84	82	58	15−210	82	20	14−28	13	59	23−125
	H25.51	103	6.2	3−10	105	8	0−29	105	7	0−28	105	45	15−105	105	26	19−34	14	98	42−188
	H25P3	99	7.3	3−10	100	17	0−129	100	15	1−118	100	39	6−104	100	23	7−43	18	150	75−278

[a] Number of plants analyzed. [b] Asparagine concentration not analyzed in empty cells.

and 5 mL of 15−8−11 Osmocote (The Scotts Co., Marysville, OH) extended release fertilizer. The 10 cm pots were used as stressors to initiate tuberization in wild potato species, many of which are photoperiod sensitive and not adapted to northern latitudes. Fifteen plants per accession were placed in a flat in a hoophouse at Rhinelander, WI, and in a coldframe in Madison, WI, in a completely randomized design when all danger of freezing was past. Mean daily temperatures from May to September at Rhinelander, WI, were on average 1.6 °C lower than at Madison, WI. Temperatures in 2005, 2006, and 2007 were similar and ∼2.8 °C warmer than 2004. Plants grown outdoors at Madison, WI, experienced record precipitation in May 2004 (15.3 cm) and August 2007 (25.4 cm). Plants were watered and fertilized as necessary from May until late September or October, or senescence, whichever occurred first. Water was withheld from visibly senescing plants, and their tubers were harvested when leaves senesced. Plants that did not senesce were allowed to grow until late September or early October, at which time water was withheld and tubers were harvested in mid-October. Tubers were placed in paper bags and moved to a storage locker at 2 °C and >90% relative humidity within a week of harvest.

Storage and Analysis of Tubers. Tubers were stored for 3 months and chip processed within an hour of removal from 2 °C storage. Two tubers from each plant were assayed. Tubers were sliced in half from apical end to basal bud, and a 2−3 mm slice from each half was fried in vegetable oil (Crisco vegetable oil, J. M. Smucker Co., Orville OH). If the tuber was <5 mm in diameter, each half was fried. Within 10 min of preparation, all slices were fried at 190 °C in a commercial fryer until bubbling ceased. Chips were scored within 5 min of completion by using the Potato Chip Institute International Color Chart, where a score of 1 is lightest and 10 is darkest. Values as high as 4.5 were once considered to be acceptable in some studies (*26*), but with the industry today demanding chip scores of <3, this study interpreted chip color scores as best (1−3), acceptable (4−5), marginal (6−7), and poor (8−10) (*9*, *20*). The average color of four chips was the "chip score" for each plant.

Tissue for carbohydrate and amino acid analysis was collected from tubers stored at 2 °C within the time frame described for chip color analysis. Fresh weight (FW) of tuber pieces remaining from chip color samples and/or other tubers from the same plant was recorded to the nearest milligram. Tissue was frozen at −80 °C, lyophilized, and weighed again for dry weight (DW). Percent dry matter was determined by dividing DW by FW and multiplying by 100. The periderm was removed, and the entire sample remaining was crushed to a fine powder; 0.2 ± 0.01 g was extracted twice in 4.5 mL of 80% ethanol at 60 °C for 1 day each time. Supernatants were combined and brought to a final volume of 10.0 mL.

Two milliliters of ethanol extract was evaporated to dryness under vacuum at 40 °C and resuspended in 100 μL of double-distilled water for fructose, glucose, and sucrose quantification by HPLC (Waters Corp., Milford, MA). Sugars from plants grown in 2004 and 2005 were separated at ambient temperature on a 10 μm, 300 × 4.1 mm, Alltech carbohydrate amino column (Alltech Associates Inc., Deerfield, IL), and sugars from plants grown in 2006 and 2007 were separated at ambient temperature on a Microsorb-MV 100-5 Amino 250 × 4.6 mm column (Varian Inc., Palo Alto, CA). These columns were comparable in performance. All-guard Amino Carbohydrate 10 μm cartridge guard columns (Alltech) were used in all years. The mobile phase in 2004 and 2005 was a mixture of 80% acetonitrile and 20% water, and the mobile phase in 2006 and 2007 was a 76% acetonitrile and 24% water mix. The injected volumes were 50 μL in 2004 and 20 μL in the following years. A 2.0 mL min^{-1} flow rate was used in 2004 and 2005, but was reduced to 1.6 mL min^{-1} in 2006 and 2007. Total run time was 16 min in all years. Sugars from plants grown in 2004 were detected using a Waters 401 refractive index detector at an attenuation of 2×. Sugars from plants grown in 2005−2007 were detected with a Shimadzu evaporative light-scattering detector−low temperature (ELSD-LT) detector at an attenuation of 2×. Chromatograms were analyzed using Shimadzu Client/Server software version 7.2 SP1 Build 9 (Shimadzu, Tokyo, Japan). Retention times and peak areas for samples were compared to those of reagent grade standards of fructose, glucose, and sucrose.

One milliliter of ethanol extract was evaporated to dryness under vacuum at 40 °C and resuspended in 7.9 mL of 20 mM HCl for amino acid separation on a Waters HPLC. Samples were derivatized using the Waters AccQ-tag kit following instructions provided by the manufacturer but scaled to one-fourth size. Derivatized samples were diluted with three

Table 3. Correlation of Tuber Fructose Concentration with Glucose Concentrations after 3 Months of Storage at 2 °C

species	PI or ID	*N*	correlation[a]
S. acaule	472752	42	0.92 ***
S. berthaultii	275154	135	0.77 ***
	473239	229	0.86 ***
S. chacoense	175443	168	0.79 ***
	472826	198	0.79 ***
S. circaeifolium	473458	43	0.77 ***
S. kurtzianum	473420	151	0.95 ***
S. lignicaule	498253	41	0.96 ***
S. okadae	320327	45	0.97 ***
	498063	45	0.96 ***
S. oplocense	473368	111	0.69 ***
S. phureja	225673	26	0.97 ***
S. pinnatisectum	347766	272	0.73 ***
	537023	165	0.64 ***
S. raphanifolium	458384	114	0.81 ***
S. sogarandinum	230510	41	0.93 ***
S. sparsipilum	458385	101	0.75 ***
	458386	90	0.85 ***
S. stoloniferum	283100	117	0.88 ***
	498035	71	0.88 ***
S. tuberosum ssp. *andigenum*	281222	30	0.88 ***
	285005	21	0.80 ***
S. tuberosum	Snowden	127	0.84 ***

[a] Level of significance: ***, $P \leq 0.0001$.

parts water prior to separation on a 4 μm, 3.9 × 150 mm, 60 Å Nova-Pak C18 column fitted with 4 μm, 3.9 × 20 mm, 60 Å Nova-Pak C18 guard column. The column temperature was held at 37 °C using a Fiatron CH-3 column heater. An injection volume of 30 μL at a flow rate of 1.0 mL min^{-1} for 76 min was used. The mobile phase was a mixture of (A) 12.5 mM sodium phosphate (pH 6.3) and (B) 12.5 mM sodium phosphate (pH 6.3) and acetonitrile (70:30). The gradient of mixture A to mixture B was as follows: 100:0 for 30 s; 93:7 for 4 min; 90:10 for 14 min; 68:32 for 7 min; 60:40 for 24 min; 0:100 for 26 min using a linear transition curve. A Shimadzu RF-10A XL fluorescence detector ($\lambda_{excitation}$ = 250, $\lambda_{detection}$ = 395) detected the derivatized amino acids. Retention times and peak areas for samples were compared to an internal 0.1 mM aminobutyric acid standard, external 0.1 mM asparagine, and a 0.1 mM mixture of 20 amino acids standards using Waters Empower Build 1154 + service packs 1 and 2 software (Waters Corp.).

Statistical analysis was conducted using SAS Statistical Software version 9.1.3 (SAS Institute Inc., Cary, NC). A mixed model in Proc MIXED was used to determine if accession chip color and tuber composition differed significantly after accounting for nongenetic effects in data combined over years, locations, and propagation methods. PI was the fixed effect, whereas random effects included location, years, and interactions between locations, years, and PIs. Chip color, fructose, glucose, sucrose, and asparagine were each individually used as dependent variables in the mixed model. The Satterthwaite correction was used to calculate denominator degrees of freedom. Proc GLM was used for all regressions, and $P < 0.05$ was required for entry into stepwise regressions.

RESULTS AND DISCUSSION

Chip Color. Light chip color was not common when slices from tubers stored at 2 °C were fried (**Figure 1**). When chip scores were evaluated as in refs *9* and *20*, 80 (2%), 531 (15%), 1225 (35%), and 1665 (47%) plants had best (color scores of 1−3), acceptable (scores of 4−5), marginal (scores of 6−7), and poor (scores of 8−10) chip color, respectively. Overall, 17% of the plants analyzed produced tubers that chipped acceptably (color scores of ≤5), and this percentage was much higher than that in earlier studies, where 2.5% of plants from wild *Solanum* accessions (*20*) and 7% of progeny from species-haploid crosses (*27*) had chip color scores of < 5. The greater number of plants producing acceptable chips in this experiment most likely reflects the preferential

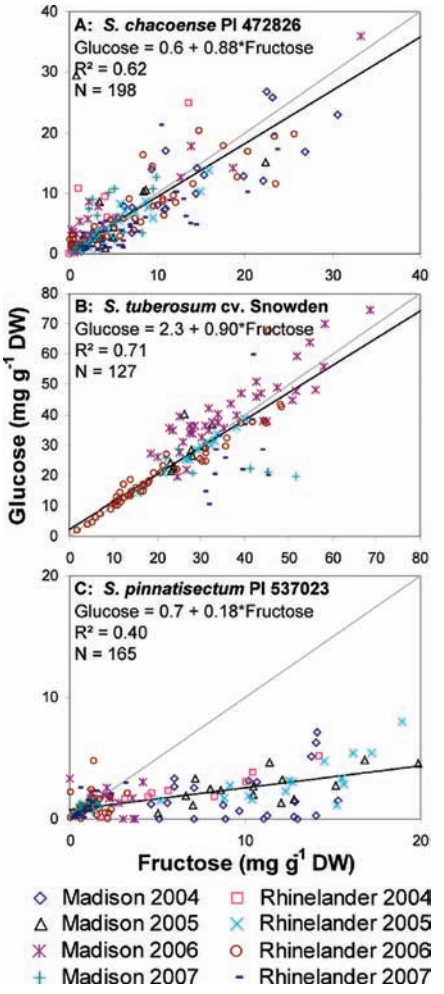

Figure 2. Typical relationships between tuber fructose and glucose concentrations in wild *Solanum* species and cultivated potato as illustrated by *S. chacoense* (**A**) and *S. tuberosum* (**B**), where both sugars were in approximately equal amounts, and in *S. pinnatisectum* (**C**), where tuber fructose was much greater than tuber glucose content. Light gray lines indicate the ratio of 1:1 that is expected if glucose and fructose accumulate as a result of acid invertase activity, and the dark gray line is the best fit of the linear regression.

inclusion of accessions identified by Hanneman and co-workers as producing light chips from 2 °C storage (*20*). The experimental conditions used in this study were likely to enhance expression of the dark chip color phenotype because plants grew under stressful conditions and tubers were stored at extremely cold temperatures (2 °C). Previous research suggests that the greenhouse-grown accessions evaluated in this study would have lower tuber reducing sugar content and lighter chip color when grown under less stressed conditions (*28*).

Chip color was highly variable within each of the 53 accessions that were evaluated over four years at two locations (**Figure 1**). Seventy-five percent of the accessions included at least one plant with tubers that chipped below an average score of 5, but 93% of the accessions also included at least one plant with a chip color score of > 8 (**Table 2**). Accession mean chip color ranged from 4.9 to 9.3 with significant differences among accessions ($F = 7.4$, $P \leq 0.001$). All accessions of *S. medians*, *S. piurae*, *S. raphanifolium*, and *S. sogarandinum* and some accessions representing *S. chacoense*, *S. multiinterruptum*, *S. okadae*, and *S. pinnatisectum* had accession mean chip scores below 6.5. These species were previously identified as sources of light chip color (*20*). Chip color

Table 4. Correlation of Chip Color with Tuber Composition after 2 °C Storage for 3 Months[a]

			mg g^{-1} of DW				μmol g^{-1} of DW			
species	PI or ID	N[b]	fructose	glucose	reducing sugars	sucrose	N[c]	asparagine	N[d]	% dry matter
S. acaule	472752	34	**0.77** ***	0.46**	**0.77** ***	0.05 NS	28	−0.13 NS	25	−0.57 **
S. berthaultii	275154	129	0.46 ***	0.49***	**0.50** ***	−0.03 NS	69	0.20 NS	93	−0.31 **
	473239	222	0.65 ***	0.58***	**0.67** ***	0.23 ***	74	0.08 NS	184	−0.38 ***
S. chacoense	175443	157	0.57 ***	0.63***	**0.63** ***	0.20 *	79	−0.13 NS	138	−0.28 ***
	472826	192	**0.69** ***	0.57***	0.66 ***	0.39 ***	70	−0.07 NS	168	−0.24 **
S. circaeifolium	473458	31	0.43*	0.54**	**0.55** **	0.09 NS	29	−0.20 NS	12	−0.30 NS
S. kurtzianum	473420	144	**0.50** ***	0.46***	0.49 ***	0.13 NS	81	−0.05 NS	121	−0.31 ***
S. lignicaule	498253	30	0.45 *	0.52**	**0.52** **	0.21 NS	21	0.09 NS	15	−0.14 NS
S. okadae	320327	26	**0.68** ***	0.68***	**0.68** ***	0.01 NS	25	0.19 NS	14	0.11 NS
	498063	24	0.20 NS	0.22NS	0.18 NS	0.17 NS	23	0.02 NS	18	−0.09 NS
S. oplocense	473368	107	0.54 ***	0.58***	**0.62** ***	−0.18 NS	55	0.14 NS	81	−0.34 **
S. phureja	225673	20	0.58 **	0.62**	0.62 **	0.07 NS	20	0.40 NS	11	0.36 NS
S. pinnatisectum	347766	264	−0.03 NS	0.04NS	0.00 NS	0.28 ***	206	**0.30** ***	247	−0.22 ***
	537023	159	−0.01 NS	−0.02NS	−0.04 NS	**0.16** *	153	0.14 NS	131	−0.01 NS
S. raphanifolium	458384	100	0.43 ***	**0.47****	**0.47** ***	0.04 NS	61	0.22 NS	80	−0.25 *
S. sogarandinum	230510	31	**0.69** ***	0.55**	0.63 ***	0.48 **	25	−0.33 NS	27	−0.49 **
S. sparsipilum	458385	93	0.43 ***	**0.55****	0.52 ***	0.03 NS	87	−0.01 NS	65	−0.25 *
	458386	85	**0.78** ***	0.59***	0.78 ***	−0.07 NS	49	0.03 NS	64	0.03 NS
S. stoloniferum	283100	114	**0.50** ***	0.41***	0.47 ***	0.24 **	63	0.14 NS	91	−0.25 *
	498035	62	0.60 ***	0.62***	0.61 ***	−0.16 NS	59	−0.01 NS	32	**-0.64** ***
S. tuberosum	281222	25	0.17 NS	0.19NS	0.19 NS	0.05 NS	17	**0.54***	10	−0.36 NS
ssp. andigenum	285005	21	0.48 *	0.65**	0.62 **	0.18 NS	20	−0.02 NS	16	−0.49 NS
S. tuberosum	cv. Snowden	127	**0.71** ***	0.65***	0.70 ***	0.35 ***	22	0.30 NS	126	−0.53 ***

[a] The highest significant correlation for each accession is in bold. Levels of significance: ***, $P \leq 0.0001$; **, $P \leq 0.01$; *, $P \leq 0.05$; NS, $P > 0.05$, not significant. [b] Number of plants analyzed for chip color and tuber sugar composition from 2004 to 2007. [c] Number of plants analyzed for chip color and asparagine concentrations is less because asparagine was not analyzed for all plants in 2006 and 2007. [d] Number of plants analyzed for chip color and percent dry matter in 2005, 2006, and 2007.

of *S. tuberosum* cv. Snowden ranged from 6 to 10, making Snowden a relatively uniform accession with dark chip color. All wild species accessions except *Solanum stoloniferum* PI 283100 had mean chip color scores lower than that of Snowden, and all except two accessions had plants that produced chips that were lighter in color than the lightest from Snowden (**Figure 1**). Thus, practically every wild accession included a plant that produced light-colored chips and could be used as a parent in a breeding program if enough plants were assayed (**Table 2**). All PIs of *S. acaule*, *S. circaeifolium*, *S. iopetalum*, *S. kurtzianum*, *S. lignicaule*, *S. oplocense*, *S. phureja*, *S. sparsipilum*, *S. stoloniferum*, *S. berthaultii*, and *S. tuberosum* ssp. *andigenum* produced chips with a mean chip score of ≥6.5. Although some of these species have been used in potato breeding programs, they are not likely sources of genetic diversity useful to breed for light chip color from tubers held at 2 °C cold storage because of a prevalence of dark chip color. Species with a greater frequency of light chip color are more likely sources of genetic diversity for rapid improvement of this trait.

Reducing Sugar Concentration. Tuber reducing sugar concentrations varied greatly among and within accessions, including those that were clonally propagated (**Figure 1**). Fructose and glucose concentrations ranged from none detected to 327 mg g^{-1} of DW in tubers from individual plants (**Table 2**). Low reducing sugar (the sum of fructose and glucose) concentration as defined by the industry (**Table 1**) was rare in tubers from 2 °C cold storage. Only 2% of 3502 plants had tuber reducing sugar concentration below 0.35 mg g^{-1} of DW, although 29% of plants had reducing sugars of < 5 mg g^{-1} of DW. Accession mean reducing sugar concentrations ranged from 1 to 85 mg g^{-1} of DW (**Figure 1**) with significant differences among accessions ($F = 8.9$, $P \leq 0.001$). Mean reducing sugar concentration in some *S. chacoense*, *S. pinnatisectum*, *S. raphanifolium*, and *S. sogarandinum* PIs was < 10 mg g^{-1} of DW. Only *S. pinnatisectum* and *S. raphanifolium* accessions had mean reducing sugar concentrations of < 5 mg g^{-1} of DW. Genotypic variation within most accessions could be utilized in breeding, therefore, for low reducing sugar concentration if enough plants were evaluated in fine screens of germplasm using multiyear evaluations.

Sucrose, Asparagine, and Percent Dry Matter. Sucrose and asparagine concentrations and percent dry matter varied widely among and within accessions. Mean sucrose concentrations ranged from 21 to 158 mg g^{-1} of DW among accessions (**Table 2**) with significant differences among accessions ($F = 12.2$, $P \leq 0.001$). Because sucrose does not react directly in the Maillard reaction (*29*), sucrose concentrations *per se* have rarely been emphasized in chip color studies. Average asparagine concentrations ranged from 23 to 288 μmol g^{-1} of DW (**Table 2**), but accessions did not differ significantly ($F = 1.1$, $P = 0.42$) because of large environmental and intra-accession variance. Accession mean percent dry matter ranged from 18 to 35% (**Table 2**) with significant differences among accessions ($F = 8.6$, $P \leq 0.001$). High dry matter is desirable in chipping potatoes because raw product with high dry matter content absorbs less oil during frying than product with lower dry matter content.

Tuber Reducing Sugar Profiles. Tuber sugar profiles varied by accession. Glucose concentrations significantly correlated with fructose concentrations for all accessions (**Table 3**). Glucose and fructose concentrations were approximately equal in most accessions of wild *Solanum* species and in *S. tuberosum* cv. Snowden (**Figure 2A**,**B**). These data are consistent with invertase cleaving sucrose to glucose and fructose in cold-stored tubers of wild and cultivated *Solanum* (*3*, *5*, *9*, *30*, *31*). In *S. acaule* and *S. pinnatisectum*, however, fructose concentration exceeded glucose concentration (**Figure 2C**). Higher concentrations of fructose than glucose could occur if glucose resulting from invertase-mediated sucrose cleavage was preferentially cycled into carbon metabolism or respiration. Alternatively, unequal amounts of fructose and glucose could occur if sucrose synthase rather than invertase broke down sucrose during cold storage. In that case, fructose and UDP-glucose, not fructose and free glucose, would accumulate. In either case, *S. acaule* and *S. pinnatisectum* represent novel

natural sources to evaluate carbon cycling and the regulation of CIS in future studies. Likewise, CIS at 2 °C may be regulated differently in those accessions with low mean reducing sugar concentrations than in accessions with high mean reducing sugar concentration.

Relationships between Tuber Composition and Chip Color. Regressions of chip color with the natural log of fructose, glucose, sucrose, or asparagine content and percent dry matter differed among accessions as reflected by changes in intercept, slope, fit of the regression (R^2), and significance. The natural logarithms of sugar contents were used to optimize linear regressions. Likewise, correlation coefficients of tuber composition with chip color varied in magnitude and significance within species represented by multiple accessions (**Table 4**).

Positive curvilinear relationships between chip color and glucose or fructose concentrations existed for most accessions (**Figure 3A**,**B**). Changes in reducing sugar content at low concentrations of either reducing sugar had a much larger effect on chip color than equal changes at high concentrations of reducing sugars. For all accessions, chips with the same color were produced from tubers having a range of reducing sugar concentrations. For example, plants of *S. chacoense* PI 472826 with a chip color score of 7 had tuber glucose concentrations of 1−26 mg g^{-1} of DW. This suggests that browning in the Maillard reaction depends on reducing sugar concentrations in conjunction with other tuber metabolites.

Fructose and glucose concentrations significantly correlated to chip color in the majority of accessions (**Table 4**). The average correlation coefficient of chip color with reducing sugars in this study was 0.47, which was at the lower end of previously reported correlations (r = 0.46−0.92) for cultivated potato (*2*, *32*, *33*). Neither reducing sugar significantly correlated with chip color in some accessions of *S. okadae* and *S. pinnatisectum* (**Figure 3C**), which is consistent with the observation that chip color does not correlate with extremely low concentrations of reducing sugars in raw tubers (*2*, *5*). Tubers from *S. tuberosum* cv. Snowden, which was clonally propagated, varied as much in tuber composition and chip score as presumably genotypically heterogeneous PIs. Tubers from *S. tuberosum* cv. Snowden had a significant correlation coefficient of chip color with reducing sugars (N = 127, r = 0.71, $P \leq 0.001$) that was comparable to those in previously published studies. Genotypic variation confounded with environmental variance may partially explain lower correlation coefficients of tuber sugar concentrations with chip color in wild *Solanum* species. Total reducing sugar concentration did not account for more variation in chip color than fructose or glucose concentrations alone (**Table 4**), likely because fructose and glucose concentrations were highly correlated in most accessions (**Table 3**).

Tuber sucrose concentration significantly correlated to chip color in 22 of 42 accessions with more than 15 observations. The correlation of sucrose concentration with chip color was lower than that of reducing sugars with chip color (**Table 4**), and this is consistent with previous findings (*2*, *8*, *9*, *32*, *33*). Sucrose concentrations significantly correlated to chip color in some accessions of *S. pinnatisectum*, which supports the hypothesis that hydrolysis of sucrose may occur during frying and that these newly created reducing sugars contribute to chip darkening (*34*). Almost all significant correlations of sucrose concentration with chip color were positive, suggesting that sucrose does not inhibit the Maillard reaction and that its hydrolysis products contribute to chip color.

In cultivated potato, reducing sugar concentrations are commonly thought to limit the Maillard reaction (*6*). In tubers from diverse *Solanum* species, the mean molar ratio of reducing sugars

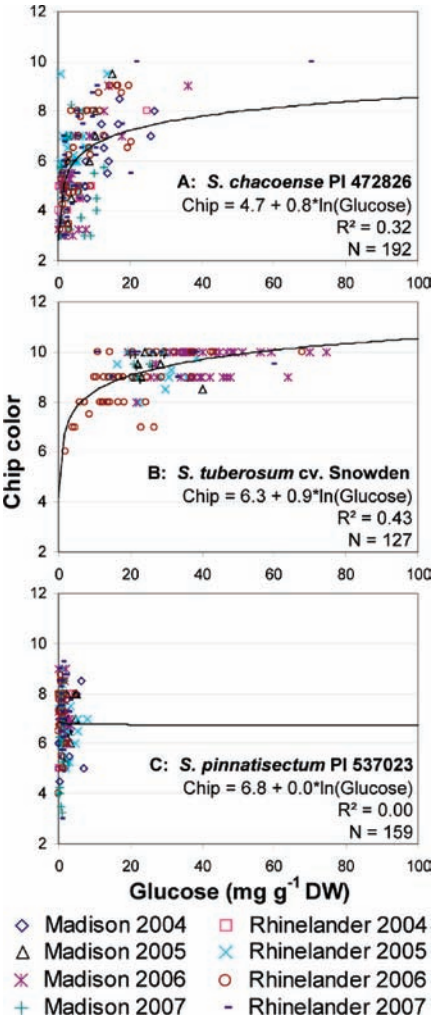

Figure 3. Relationships between chip color and glucose concentration.

to asparagine was typically >1 and exceeded 1.25 in 35 of 47 accessions. Asparagine was the predominant amino acid in cold-stored tubers of wild *Solanum* species (data not shown). If asparagine concentration limits pigment formation in the Maillard reaction in some accessions, then asparagine concentration should correlate to chip color for those accessions. Asparagine concentration rarely correlated to chip color (**Table 4**), however, and these data are consistent with previous studies of potato cultivars showing that amino acid content is not rate limiting for the Maillard reaction (*7*−*9*, *35*, *36*). Exceptions to this were weak correlations of asparagine concentration with chip color in multiple *S. pinnatisectum* accessions (r = 0.19−0.31) and higher correlations in *S. tuberosum* ssp. *andigenum* (r = 0.54).

Percent dry matter significantly and negatively correlated to chip color in 27 of 42 accessions (**Table 4**). This was inconsistent with previous results, where chip color did not correlate with dry matter (*2*, *32*). Dark chip color at low percent dry matter (high water content) seems counterintuitive with the Maillard reaction occurring in high-heat, dehydrating cooking conditions. The percent dry matter in raw tubers in this study did not reflect the extremely low or surplus water content that inhibits the Maillard reaction (*29*, *37*). Tuber percent dry matter *per se* likely influenced cooking duration and thus may have indirectly affected the extent of browning on the surface area of the chip. To counter this confounding effect, some researchers do not fry until bubbling ceases but use moisture content of the fried product to determine when to terminate frying (*38*).

Table 5. Stepwise Multiple Linear Regressions of Tuber Sugar Concentrations (Milligrams per Gram of DW) with Chip Color

				partial R^2		
species	PI or ID	*N*	total R^2	fructose	glucose	sucrose
S. *acaule*	472752	34	**0.59**	0.59	a	
S. berthaultii	275154	129	**0.24**		0.24	
	473239	222	**0.45**	0.42	0.02	0.01
S. chacoense	175443	157	**0.41**	0.02	0.40	
	472826	192	**0.48**	0.47		0.01
S. circaeifolium	473458	31	**0.29**		0.29	
S. kurtzianum	473420	144	**0.25**	0.25		
S. lignicaule	498253	30	**0.27**		0.27	
S. okadae	320327	26	**0.47**	0.47		
	498063	24	**0.00**			
S. oplocense	473368	107	**0.42**	0.04	0.34	0.03
S. phureja	225673	20	**0.39**		0.39	
S. pinnatisectum	347766	264	**0.08**			0.08
	537023	159	**0.03**			0.03
S. raphanifolium	458384	100	**0.22**		0.22	
S. sogarandinum	230510	31	**0.46**	0.46		
S. sparsipilum	458385	93	**0.30**		0.30	
	458386	85	**0.61**	0.61		
S. stoloniferum	283100	115	**0.32**	0.25		0.07
	498035	61	**0.39**		0.39	
S. tuberosum ssp.	281222	23	**0.00**			
andigenum	285005	21	**0.42**		0.42	
S. tuberosum	cv. Snowden	127	**0.51**	0.51		

[a] Variables with $P > 0.05$ did not enter the stepwise multiple linear regression and have empty cells.

The relationship of chip color to tuber composition was examined with multiple linear regressions for each accession. Asparagine concentration and percent dry matter did not significantly account for chip color variation because tuber sugar concentrations entered the model first for most accessions. Fructose or glucose concentrations accounted for the majority of chip color variation that could be explained (**Table 5**). When glucose and fructose were both present in the equation, one sugar accounted for the majority of variation, whereas the remaining sugar explained a minor portion. For the data set as a whole, fructose contributed the largest partial R^2 value in 20 accessions and glucose in 15 accessions. For those accessions included in **Table 5**, fructose contributed the largest partial R^2 value in 9 accessions and glucose in 10 accessions. Sucrose concentration typically accounted for a minor portion of chip color variation after reducing sugars, which is consistent with previous findings (*6*). The fit of the multiple linear regressions (R^2) was low, and a single variable accounted for most chip color variation. It is notable that *S. okadae* PI 498063, which had the lowest average chip color of any accession evaluated and relatively low reducing sugar concentrations (**Table 2**), *S. pinnatisectum* PI 347766, which had the lowest reducing sugar concentrations evaluated with marginal chip color scores, and *S. tuberosum* ssp. *andigenum* PI 281222, which had relatively high chip color scores and reducing sugar concentrations (**Figure 1**), all had very low total R^2 values ranging from 0 to 0.08 (**Table 5**). Quantifying fructose, glucose, and sucrose concentrations in cold-stored potato tubers is not likely, therefore, to be an effective means of predicting chip color, especially in exotic germplasm.

In conclusion, tuber sugar composition in wild *Solanum* may address questions about the physiological response of wild *Solanum* to cold storage or the Maillard reaction, but tuber composition was a poor predictor of chip color. Invertase-mediated sugar accumulation appeared to occur in cold-stored wild and cultivated *Solanum* with the exception of *S. pinnatisectum*. Excess fructose relative to glucose concentration and extremely low reducing sugar and high sucrose concentrations in *S. pinnatisectum* present a unique opportunity to examine invertase regulation or function in CIS relative to other *Solanum* species. Tuber reducing sugar and sucrose concentrations partially explained chip color variation for most accessions evaluated, but tuber asparagine concentration and percent dry matter did not. The wide range of chip color scores and tuber composition observed among clonally propagated plants recommends multiple year and/or location evaluations to obtain accurate data. On the basis of our results, high tuber fructose and glucose concentrations after 2 °C cold storage ($> \sim 30$ mg g^{-1} of reducing sugar DW) are reliable indicators of high chip color scores, but lower concentrations are not effective predictors of light chip color in diverse *Solanum*. The identities of compounds responsible for elevated chip color scores when free sugars and amino acids are low remain unidentified.

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