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Potential for improvement by selection for reducing sugar content after cold storage for three potato populations

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Abstract The objectives of this study were to examine the expected response to selection for reducing-sugar content after cold storage in three hybrid populations, to determine whether these populations included clones low in reducing sugars, and to investigate the effectiveness of indirect selection for chip colour based on selection of sugar content after cold storage. The three hybrid populations included: a random sample of 39 clones of Population 1, which was derived from crossing ND860-2 (a clone low in reducing sugars) with F58089 (a clone intermediate in reducing sugars); 40 clones of Population 2, which was obtained from crossing ND860-2 with Russette (a clone high in reducing sugars); and 40 clones of Population 3, which was derived from crossing Russette with F58089. Sugar content and chip colour were assessed in tubers stored for 2 months at 4 °C at Cambridge, Ontario, and at 3 °C at Benton Ridge, New Brunswick. Population 1 had a slightly greater predicted response to selection for reduction in glucose and total reducing sugars than the other two populations. This could be attributed to higher heritability estimates for Population 1, which was a reflection of smaller clone × environment interaction mean squares. The greater potential advance by selection for fructose, glucose, and total reducing sugars, was a direct consequence of its lower means for these traits. Low reducing-sugar clones were found in all three populations, indicating their potential use for the selection of low reducing sugars. Populations 2 and 3, however, would require stronger selection pressures and, therefore, large population sizes. Expected correlated responses for chip colour by selection for fructose and glucose were similar to, and sometimes exceeded, the expected direct responses in all three populations. Indirect responses for chip colour by selection for sucrose, however, were lower than direct selection responses. These results indicate that indirect selection for chip colour, by selection for either fructose or glucose content after cold storage, is as effective as direct selection for chip colour.

Key words Sugar · Chip colour · Processing · Storage
Selection response · Indirect selection
Solanum tuberosum

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Introduction

Reducing-sugar content (fructose and glucose) is a major quality factor in potato processing. The browning of potato chips is primarily the result of the Maillard reaction between aldehyde groups of reducing sugars and the free amino groups of the amino acids and proteins during the frying process (Talburt et al. 1975), with the amount of reducing sugars being the limiting factor (Marquez and Añon 1986). The contribution of sucrose to non-enzymatic browning in potato chips has been postulated by some authors (Shallenberger et al. 1959; Leszkowiat et al. 1990). The sugar content in potato tubers, and the consequent chip colour, depend on both genetic and environmental factors (Stevenson et al. 1954). Tubers of most chipping cultivars stored at temperatures below 9–10 °C accumulate appreciable amounts of sugars due to a phenomenon known as low-temperature sweetening (Burton 1969; Coffin et al. 1987). The reducing sugars reach a maximum level after about 4 to 8 weeks of cold storage (Schwimmer et al. 1954; Burton and Wilson 1978; Barichello et al. 1990). There are,

however, some clones which maintain a low reducing-sugar content at low temperatures (Coffin et al. 1987; Johansen 1987; Colon et al. 1989; Brown et al. 1990; Ehlenfeldt et al. 1990).

The development of processing cultivars with low levels of reducing sugars during cold storage is receiving high priority in potato breeding programs in North America. This is, in part, due to the fact that cultivars resistant to low-temperature sweetening would provide several economic benefits, such as less need for sprout inhibitors, reduced dry matter loss, easy maintenance of high relative humidity, less pathogen problems, and less chance of chilling injury during harvest, storage, and transit (ap Rees et al. 1981; Coffin et al. 1987). Selection of clones with low levels of reducing sugars after cold storage would be facilitated by information on the inheritance of this trait. Very little information is available, however, concerning genetic parameters of reducing-sugar content of potato tubers stored at low temperatures. Grassert et al. (1984) observed very high heritability (≥ 0.91) of the reducing-sugars after cold storage for cultivars. For segregating populations, Chitsaz (1983) found heritability of glucose content at harvest time on a clonal mean basis to be low (0.21).

The objectives of the present study were to examine the expected responses to selection for reducing sugars in three potato populations, to determine whether populations would include clones that would meet acceptable levels of reducing sugars when stored at cold temperatures (3–4 °C), and to evaluate the effectiveness of indirect selection for chip colour based on sugar content.

Materials and methods

Hybrid populations derived from crosses among three parents were used in this study. The parental clones were deliberately chosen to represent a range in reducing-sugar content and other quantitative traits (maturity, yield, specific gravity, tuber size, and dormancy). F58089 is a regular storage chipping clone, which was developed by Agriculture Canada, Fredericton. ND860-2 is a clone that accumulates low quantities of sugars in cold storage, and was developed at North Dakota State University (Johansen 1987). Russette has an inherently high sugar content, and was released by the USDA, Beltsville (Webb et al. 1984). Population 1 was derived from the cross of ND860-2/F58089, female and male parent, respectively; Population 2 was obtained from the cross of ND860-2/Russette; and Population 3 was derived from the cross of Russette/F58089. The parent clones plus seven other cultivars ranging broadly in sugar content (Atlantic, F58050, Fundy, Katahdin, Kennebec, Norchip, Superior) were also evaluated in the experiments as checks.

Potatoes were grown in two environments: Cambridge, Ontario, 1990; Benton Ridge, New Brunswick, 1991. At Cambridge, the soil was a Fox sandy loam. Fertilizers were applied at the time of planting at the rate of 128 N, 64 P and 64 kg ha^{-1} K. Uniform seed pieces were planted on 15 May and tubers were harvested on 19 September, 2 weeks after top-killing. Irrigation was applied as needed to supplement natural rainfall. At Benton Ridge, the soil was a Carleton loam and was fertilized at planting time with 145.5 N, 97 P, 97 K, and 29.1 kg ha^{-1} Mg. Planting was on 21 May and tubers were harvested on 4 October, when senescence from the desiccant was complete. No irrigation was provided. Pest control and other cultural practices were similar to the commercial plantings in the areas.

Fifty-five randomly-selected clones from each cross were grown at Cambridge in 1990, and 100 clones at Benton Ridge in 1991. The clones tested at Benton Ridge included the 55 clones tested at Cambridge. The experimental design was an augmented block (Federer and Raghavarao 1975). Clones of the three hybrid populations were nonreplicated and randomly distributed in the experiment, whereas the ten check cultivars were repeated four times in a randomized block design. The experimental unit for clones and check cultivars consisted of single five-hill plots spaced at 91.4 cm apart between rows and individual plants spaced 25.4 cm apart within a row. A sample of 39 clones from Population 1 and 40 clones of Populations 2 and 3, as well as the replicated check cultivars, were used for sugar content assessment. All clones were grown in both experiments. Harvested tubers were stored for 2 months at 4 °C and 3 °C, 90–95% RH, at Cambridge and at Benton Ridge, respectively.

Samples for sugar assessment and chip-colour evaluation consisted of three medium-size (57–89 mm diameter) tubers.

For sugar analysis, a tissue sample from the midsection of each tuber of the three-tuber sample was taken, using a cork borer (8 mm diameter). The extraction and measurement of sugars (fructose, glucose and sucrose) followed the method of Wilson et al. (1981), using high performance liquid chromatography (HPLC). The juice was extracted by grinding a sample of 10 *g* of tissue in 8 ml of HPLC-grade methanol with an Ultra Turrax homogenizer (Type-TP 18/1059, Janke and Kunkel GmbH and Co. Kg Ika-Werk D7813 Staufen). Fructose, glucose and sucrose were determined on the basis of duplicate HPLC injections of each sample. Quantification of the three sugars was obtained from standard curves, using peak heights.

For chip colour evaluation, five 1-mm-thick slices were cut from the midsection and adjacent to the holes left from sampling for sugars. A total of 15 slices from each sample were cut, washed in cold water, dried on paper towel, and fried in hydrogenated vegetable oil at about 180 °C until bubbling ceased. After draining and cooling, the chips were scored for colour using Agriculture Canada Chip Colour Charts (10–100). Readings of 50 or greater are defined as acceptable for processing (Coffin et al. 1987).

For each hybrid population and check cultivars, analyses of variance for fructose, glucose, total reducing sugar (fructose + glucose), and sucrose content combined across environments were performed. Analyses of data from check cultivars provided the estimates of the experimental error for testing clone × environment mean squares. Variance components were estimated by equating appropriate mean squares to their expectations and solving for the components. Expected mean squares were based on a random effects model for locations and clones (Table 1). Genetic variances among clones ($\hat{\sigma}^2_g$), genotype × environment variances ($\hat{\sigma}^2_{ge}$), and heritabilities (h^2) on a plot basis were estimated as:

$$h^2=\hat{\sigma}^2_g/\hat{\sigma}^2_p=\hat{\sigma}^2_g/(\hat{\sigma}^2_g+\hat{\sigma}^2_{ge}+\hat{\sigma}^2_e)$$

$$\hat{\sigma}^2_g=(M_C-M_{CE})/E$$

$$\hat{\sigma}^2_{ge}=M_{CE}-M_e$$

$$\hat{\sigma}^2_e=M_e$$

where M_C=mean square for clones, M_{CE}=mean square for clone × environment interaction, respectively; E=number of environments;

Table 1 Form of analysis of variance and mean square expectations for clones within a population

Source	Degrees of freedom[a]	Mean square[b]	Mean square expectation[c]
Environments (E)	$E-1$		
Clones (C)	$C-1$	M_C	$\sigma^2_e+\sigma^2_{ge}+E\sigma^2_g$
C×E	$(C-1)(E-1)$	M_{CE}	$\sigma^2_e+\sigma^2_{ge}$
Error			σ^2_e

[a] E, C are the number of environments and clones, respectively
[b] M_C and M_{CE} are the observed values of the mean squares for clones and clone × environment interaction, respectively
[c] σ^2_e, σ^2_g, and σ^2_{ge} are the components of variance for error, genotype, and genotype × environment interaction, respectively
[d] Mean square from the analysis of variance of the check cultivars

Table 2 Combined analysis of variance for reducing-sugar content after cold storage for 2 months for ten check cultivars grown at Cambridge, Ontario, 1990, and Benton Ridge, New Brunswick, 1991

Source	*df*	Fructose (F)		Glucose (G)		F+G	
		Mean square	*P*-value	Mean square	*P*-value	Mean square	*P*-value
Environment (E)	1	49.85	≤0.001	55.74	≤0.001	210.37	≤0.001
Cultivars (C)	9	8.90	0.002	11.96	0.001	41.26	0.002
C×E	9	1.11	≤0.001	1.21	≤0.001	4.53	0.001
Replications/E	6	0.11	0.99	0.13	0.99	0.48	0.99
Error	54	0.13		0.17		0.55	

Table 3 Combined analysis of variance for reducing-sugar content after cold storage for 2 months for clones of three potato populations grown at Cambridge, 1990, and Benton Ridge, 1991

Population	Source	*df*	Fructose (F)		Glucose (G)		F+G	
			Mean square	*P*-value	Mean square	*P*-value	Mean square	*P*-value
1. ND860-2/F58089[a]	Environment (E)	1	14.85	≤0.001	19.45	≤0.001	63.30	≤0.001
	Clones (C)	38	0.68	≤0.001	0.81	≤0.001	2.94	≤0.001
	C×E	38	0.15	0.24	0.19	0.31	0.66	0.26
2. ND860-2/Russette	Environment (E)	1	39.99	≤0.001	56.53	≤0.001	191.61	≤0.001
	Clones (C)	39	1.04	≤0.001	1.22	0.002	4.41	≤0.001
	C×E	39	0.35	≤0.001	0.47	≤0.001	1.59	≤0.001
3. Russette/F58089	Environment (E)	1	18.91	≤0.001	28.42	≤0.001	93.70	≤0.001
	Clones (C)	39	0.62	≤0.001	0.85	≤0.001	2.81	≤0.001
	C×E	39	0.22	0.02	0.25	0.06	0.86	0.08
	Error[b]		0.13		0.17		0.55	

[a] Female/male parent
[b] Mean squares from the analyses of variance of the check cultivars

M_e=error mean square from the analysis of variance of the checks; $\hat{\sigma}_p^2$=phenotypic variance among clones; $\hat{\sigma}_e^2$=error variance from the analysis of the check cultivars.

Expected responses to selection (R) were computed as:

$$R=ih\hat{\sigma}_g$$

where i=standardized selection differential. A 10% selection intensity was used.

Estimates of (1–α) confidence intervals (α=10%) of heritability and response to selection were based on Tai (1989). For heritability, the confidence intervals were calculated as:

$$P\,(L_H \le h^2 \le U_H) \ge (1-\alpha)$$

$$L_H=[(F/F_U-1)/E]/\{[F/F_U-1)/E]+1\}$$

$$U_H=[(F/F_L-1)/E]/\{[F/F_L-1)/E]+1\}$$

where $F=M_C/M_{CE}$; $F_U=F_{\alpha/2,\,n1,\,n2}$, $n_1=m-1$, $n_2=(E-1)\,(m-1)$, m=number of clones; $F_L=F_{1-\alpha/2,\,n1,\,n2}$. For the expected response to selection, the confidence intervals were calculated as:

$$P\,(L_R \le R \le U_R) \ge (1-a)$$

$$L_R=i\,(L_g)^{1/2}\,(L_H)^{1/2}$$

$$U_R=i\,(U_g)^{1/2}\,(L_H)^{1/2}$$

where $L_g=(n_1\,M_c/X_U)\,[(F/F_U-1)/E]/(F/F_U)$, $X_U=X^2_{\alpha/2,\,n1}$; $U_g=(n_1\,M_c/X_L)\,[(F/F_L-1)/E]/(F/F_L)$, $X_L=X^2_{1-\alpha/2,\,n1}$.

Phenotypic (r_p) and genetic (r_g) correlations among sugars were computed from variances and covariances of the traits as:

$$r_p=MCP_{12}/(M_{C1}M_{C2})^{1/2}$$

$$r_g=\hat{\sigma}_{12}/(\hat{\sigma}^2_{g1}\,\hat{\sigma}^2_{g2})^{1/2}$$

where MCP_{12}=mean cross-product between traits 1 and 2; $\hat{\sigma}_{12}$=genetic covariance between traits 1 and 2.

Direct and correlated responses to selection on a plot basis for chipping colour by selecting at 10% intensity for sugar content were predicted.

Correlated response to selection for trait 2 by selecting for trait 1 (CR_{21}) was calculated as:

$$CR_{21}=i\,\hat{\sigma}_{g12}\,(\hat{\sigma}_{p11})^{1/2}$$

where $\hat{\sigma}_{g12}=(1/E)\,(MCP_{C12}-MCP_{CE12})$, MCP_{C12}=mean cross-product for clones, MCP_{CE12}=mean cross-product for the clone×environment interaction; $\hat{\sigma}_{p11}=(1/E)\,M_{C1}+[(E-1)/E]M_{CE1}$.

Estimates of (1–α) confidence intervals (α=10%) on a plot basis of expected correlated response were based on Tai (1986, 1989) as:

$$P\,(L_{CR} \le CR \le U_{CR}) \ge (1-\alpha)$$

$$L_{CR}=i\,[n_1\,X^2_{3\alpha/2,n1}/(X_L)^2]^{1/2}\,[\hat{\sigma}_{p12}\,F_L\,\hat{\sigma}_{e12}/\hat{\sigma}_{p11})^{1/2}]/K_L$$

$$U_{CR}=i\,[n_1\,X^2_{1-3\alpha/2,n1}/(X_U)^2]^{1/2}\,[\hat{\sigma}_{p12}-F_U\,\hat{\sigma}_{e12}/(\hat{\sigma}_{p11})^{1/2}]/K_U$$

where $\hat{\sigma}_{p12}=(1/E)\,(MCP_{C12}+[(E-1)/E]\,(MCP_{CE12}$; $\hat{\sigma}_{e12}=MCP_{CE12}$; $K_L=[1+(E-1)F_{3\alpha/2,n1,n2}]/E$; $K_U=[1+(E-1)F_{1-3\alpha/2,n1,n2}]/E$.

Results

Combined analysis of variance for fructose, glucose and total reducing-sugar content for the ten check cultivars showed highly-significant ($P \le 0.01$) mean squares for environments, cultivars and their interactions (Table 2). The analyses of variance for clones in each of the three populations showed significant mean squares for clones as analyzed from the fructose, glucose and total reducing-sugar contents (Table 3), indicating that genetic variances existed in each population. There were highly-significant dif-

Table 4 Means, genetic ($\hat{\sigma}^2_g$), genotype × environment ($\hat{\sigma}^2_{ge}$), and error ($\hat{\sigma}^2_e$) variance component estimates, with their standard errors (SE) for reducing-sugar content (mg g^{-1} fresh weight) after cold storage for 2 months for clones of three potato populations grown at Cambridge, 1990, and Benton Ridge, 1991

Trait	Population	Mean±SE	Variance components		
			$\hat{\sigma}^2_g$±SE	$\hat{\sigma}^2_{ge}$±SE	$\hat{\sigma}^2_e$±SE[a]
Fructose (F)	1. ND860-2/F58089[b]	0.94±0.10	0.26±0.08	0.03±0.04	0.13±0.02
	2. ND860-2/Russette	1.54±0.13	0.34±0.12	0.22±0.05	0.13±0.02
	3. Russette/F58089	1.66±0.10	0.20±0.07	0.10±0.05	0.13±0.02
Glucose (G)	1. ND860-2/F58089	1.16±0.11	0.31±0.09	0.02±0.05	0.17±0.03
	2. ND860-2/Russette	1.84±0.14	0.37±0.14	0.30±0.11	0.17±0.03
	3. Russette/F58089	1.97±0.12	0.30±0.10	0.08±0.06	0.17±0.03
F+G	1. ND860-2/F58089	2.11±0.21	1.14±0.34	0.11±0.18	0.20±0.04
	2. ND860-2/Russette	3.38±0.27	1.41±0.13	1.03±0.16	0.20±0.04
	3. Russette/F58089	3.63±0.21	0.97±0.33	0.31±0.22	0.20±0.04

[a] Component from the variance components of the check cultivars
[b] Female/male parent

Table 5 Point and confidence interval estimates for heritability (h^2) and expected response to selection (R) for reducing-sugar content (mg g^{-1} fresh weight) after cold storage for 2 months for clones of three potato populations grown at Cambridge, 1990, and Benton Ridge, 1991

Trait	Population	h^2	(CI)[a]	R	(CI)
Fructose (F)	1. ND860-2/F58089[b]	0.63	(0.44; 0.77)	–0.69	(–1.00; –0.42)
	2. ND860-2/Russette	0.50	(0.27; 0.67)	–0.70	(–1.10; –0.35)
	3. Russette/F58089	0.47	(0.24; 0.65)	–0.52	(–0.83; –0.24)
Glucose (G)	1. ND860-2/F58089	0.62	(0.42; 0.76)	–0.74	(–1.08; –0.46)
	2. ND860-2/Russette	0.44	(0.20; 0.63)	–0.68	(–1.13; –0.29)
	3. Russette/F58089	0.54	(0.32; 0.70)	–0.68	(–1.04; –0.37)
G+F	1. ND860-2/F58089	0.63	(0.44; 0.77)	–1.43	(–2.07; –0.90)
	2. ND860-2/Russette	0.47	(0.24; 0.79)	–1.38	(–2.44; –0.65)
	3. Russette/F58089	0.53	(0.31; 0.69)	–1.22	(–1.87; –0.64)

[a] Values in parentheses indicate 90% confidence limits
[b] Female/male parent

ferences between growing environments for all three populations. The clone × environment (C×E) interactions were tested by the error mean square from the analyses of data from check cultivars (Table 2). They were not significant in Population 1 but highly significant in Population 2 for all three traits and only significant ($P \leq 0.05$) for fructose in Population 3.

Frequency distributions of clones for both reducing sugars approximated to normality in Populations 2 and 3. The distribution of Population 1, however, was skewed ($P \leq 0.05$) towards the low parent, implying multiple gene interaction. A ND860-2 standard was used to establish the culling level for reducing-sugar content (fructose=0.62, glucose=0.89, and total reducing sugars=1.5 mg g^{-1} fresh tissue). For fructose, the maximum level was achieved with 33.3%, 5.0%, and 2.5% selection intensity; for glucose, with 33.3%, 10.0%, and 2.5% selection intensity; and for total reducing sugars, with 35.9%, 7.5%, and 2.5% selection intensity in Populations 1, 2, and 3, respectively. Among the low total-reducing-sugar clones, 21.4% in Population 1 and 33.3% in Population 2 had a sucrose content comparable to ND860-2 (i.e., ≤ 1.7 mg g^{-1} fresh tissue). The one low reducing-sugar clone in Population 3 had a high sucrose content (2.9 mg g^{-1} fresh tissue).

Reducing sugars were observed in significantly-lower quantities in Population 1 than in Populations 2 and 3 (Table 4). The means of the 2-year study for fructose were 39% and 43%, for glucose 37% and 41%, and for total reducing-sugar content 38% and 42%, lower in Population 1 as compared to Populations 2 and 3, respectively.

Variance components calculated from the mean squares of the combined analyses of variance (Table 4) showed that genetic variance components for both reducing sugars were relatively large. The genetic variances exceeded all other variance components for the individual and total reducing sugars in all populations. Both genetic and genotype × environment (G×E) variance components for the three traits were larger in Population 2 than in the other two populations. This would be expected as Population 2 was from the most divergent parents.

Heritability estimates derived from variance components are presented in Table 5. Heritability for the three traits was moderate, ranging from 0.44 to 0.63. The estimates for all traits were higher for Population 1 than for the other two populations. The confidence intervals, however, largely overlapped; therefore, the superiority of heritability estimates for Population 1 for any trait could not be confirmed.

The expected selection responses for reduction in fructose, glucose, and total reducing-sugar content at 10% intensity of selection were similar for the three populations (Table 5). The predicted response from selection for fructose ranged from –0.52 to –0.70 mg g^{-1} fresh tissue, for glucose from –0.68 to -0.74 mg g^{-1} fresh tissue, and for total reducing sugars from –1.22 to –1.43 mg g^{-1} fresh tissue. Again, the confidence intervals for fructose, glucose and total reducing sugars overlapped among the three populations, indicating a similar genetic advance due to selection. Consequently, the means of selected clones for fructose, glucose and total reducing sugars, respectively, would be much less in Population 1 (0.25, 0.42, and 0.68 mg g^{-1} fresh tissue) than in Population 2 (0.84, 1.16, and 2.00 mg g^{-1} fresh tissue) and Population 3 (1.14, 1.29, and 2.41 mg g^{-1} fresh tissue).

Correlation coefficients among fructose, glucose and sucrose are presented in Table 6. Both phenotypic and genetic correlations between fructose and glucose were high, positive, and consistent across populations. Correlations of sucrose with fructose or glucose were all very low and generally negative.

Estimates of expected correlated response to selection on a plot basis in chip colour, by selecting for low sugars after cold storage, and direct response for chip colour were higher within than combined across growing environments (Table 7). Within environments, predicted correlated responses for chip colour, by selecting for low sugar content, were lower than direct response estimates. Combined across environments, however, correlated responses in chip colour by fructose and glucose approximated, and sometimes exceeded, direct responses in all populations. In Population 1, the correlated response estimates for chip colour were 9.3 (104%) and 9.4 (106%) by selection for reduced fructose and glucose, respectively, compared to 8.9 from direct selection for chip colour. Selection for low fructose and glucose in Population 2 provided gains in chip colour of 8.4 (85%) and 8.5 (86%), respectively, compared to 9.9 from direct selection for chip colour. Selection for reduced fructose and glucose in Population 3 caused correlated responses in chip colour, of 6.3 (83%) and 7.4 (97%) compared to 7.6 gained from direct selection for chip colour. Furthermore, the 90% confidence intervals for the expected correlated response in chip colour, by selection for low reducing sugars after cold storage, and for the direct response, generally largely overlapped both within and combined across growing environments.

Table 6 Phenotypic (above diagonal) and genetic (below diagonal) correlations among sugars from the combined analyses of three potato populations grown at Cambridge, 1990, and Benton Ridge, 1991

Trait	Population	Fructose	Glucose	Sucrose
Fructose	1. ND860-2/F58089[a]	–	0.97	–0.05
	2. ND860-2/Russette	–	0.96	–0.08
	3. Russette/F58089	–	0.92	0.03
Glucose	1. ND860-2/F58089	0.99	–	0.03
	2. ND860-2/Russette	0.98	–	–0.10
	3. Russette/F58089	0.99	–	–0.09
Sucrose	1. ND860-2/F58089	0.07	0.10	–
	2. ND860-2/Russette	–0.02	–0.08	–
	3. Russette/F58089	–0.03	–0.08	–

[a] Female/male parent

Discussion

Response to selection can be used to compare populations to be included in a breeding program. In this study, responses to selection for fructose, glucose and total reducing sugars were estimated in order to compare populations.

Table 7 Point and confidence interval estimates of expected direct and correlated response to selection for chip colour after cold storage (3–4 °C) by selecting for low sugar content in tubers grown at Cambridge, 1990, and Benton Ridge, 1991, in three potato populations[a]

Selected trait	Growing environment	Population		
		1. ND860-2/F58089[b]	2. ND860-2/Russette	3. Russette/F58089
Fructose	Cambridge 1990	11.6 (8.7; 16.0)[c]	10.4 (7.8; 14.3)	7.7 (5.7; 11.5)
	Benton 1991	9.1 (6.6; 12.7)	10.8 (8.1; 14.7)	8.1 (5.8; 11.4)
	Combined	9.3 (5.7; 15.1)	8.4 (4.5; 14.3)	6.3 (3.1; 11.3)
Glucose	Cambridge 1990	12.5 (9.9; 16.7)	13.0 (10.3; 17.3)	11.2 (8.1; 14.5)
	Benton 1991	9.1 (6.6; 12.7)	10.6 (8.0; 14.5)	8.3 (6.0; 11.7)
	Combined	9.4 (5.7; 15.2)	8.5 (4.8; 14.5)	7.4 (3.8; 13.1)
Sucrose	Cambridge 1990	6.8 (5.9; 8.6)	0.2 (–0.3; 0.8)	1.2 (1.9; 2.4)
	Benton 1991	0.3 (–0.6; 1.3)	–2.5 (–3.2; –2.5)	0.3 (0.3; 0.4)
	Combined	–0.5 (–1.1; 0.1)	–1.4 (–2.4; –0.8)	1.2 (1.0; 1.6)
Chip colour	Cambridge 1990	14.5 (11.7; 18.4)	13.8 (11.1; 17.5)	11.8 (9.3; 15.1)
	Benton 1991	10.9 (7.9; 14.6)	12.5 (9.3; 16.3)	11.2 (8.1; 14.8)
	Combined	8.9 (5.6; 12.9)	9.9 (6.6; 13.8)	7.6 (4.5; 11.4)

[a] Chip colour: 10=dark, 100=light
[b] Female/male parent
[c] Values in parentheses indicate 90% confidence limits

The data from the three populations indicated that the predicted response to selection for reduction in individual and total reducing sugars would be large for all populations.

According to Simmonds (1979), the equation used to calculate the response to selection ($R=ih\hat{\sigma}_g$) implies that selection of superior clones depends upon the population mean, the selection intensity, the heritability, and the genetic variance. Heritability estimates for the total reducing sugars (0.47–0.63) were lower than that reported by Grassert et al. (1984) ($h^2 \geq 0.91$) on a mean basis from measurements in cultivars grown in four locations for 8 years. Higher estimates for all three traits were obtained for Population 1 as compared to the other two populations. This can be ascribed to the nonsignificant C×E interaction in Population 1 when compared with those in the other two populations (Table 3). The heritability estimates, however, did not differ significantly among the populations, and were high enough to indicate that genetic improvement for reducing sugars could be made through selection.

The slightly greater gain in the reduction of glucose and total reducing sugars in Population 1 than in the other populations (Table 5) can be attributed to higher heritability estimates, which was a reflection of smaller C×E interactions. The greater potential advance by selection for the three traits for Population 1 as compared to the other two populations, however, was a direct consequence of the lower means. Despite differences in genetic variance and heritability estimates for the reducing sugars among the populations, the means of fructose, glucose and total reducing sugars were also determinant factors for a moderate potential of improvement by selection in the case of Populations 2 and 3.

The frequency of clones with low reducing sugars (i.e., equal or less than those seen for the ND860-2 clone) was higher than that reported by Ehlenfeldt et al. (1990). Transgressive segregation for low reducing sugars suggests that clones with lower reducing-sugar content than ND860-2 can be readily developed. The occurrence of low reducing-sugar clones in each of the three populations indicates that they can all be used for selection for low reducing sugars. The difference in frequency of low reducing-sugar clones among the populations, however, would require stronger selection pressures on Populations 2 and 3 as compared to Population 1.

The phenotypic correlations among traits are influenced by both genotype and environment. The genetic correlation expresses the extent of relationship between genes that condition two traits (Falconer 1989). The similarity, consistency across populations, and close to unit coefficient for phenotypic and genetic correlation between fructose and glucose, suggests that the variation of these sugars appears to be conditioned by the same genetic system. The absence of genetic correlations of sucrose with fructose and glucose indicate that separate genetic systems control their levels. This confirms that reducing-sugar content and sucrose content are genetically independent, and indicates that simultaneous selection for these sugars is feasible.

In this study, populations were compared for their ability to accumulate less reducing sugars in cold storage, ignoring other traits. The choice of a population to be included in a processing cultivar development program, however, cannot simply be made on the basis of its performance for specific traits. Several important traits that were not part of this work must be taken into consideration. For other traits, the ranking of the populations examined may be very different. Population 1 had greater potential advance by selection for reducing sugars than the others as a result of its low initial means. The superiority for reducing sugars of Population 1, however, does not imply that this population would allow the improvement of other traits. On the other hand, Population 2, which seemed to have been derived from parents genetically more diverse for other traits as compared to Population 1, may have a large variation for other traits. Even Population 3, which had the highest means and lowest frequency of low reducing-sugar clones, should be considered because it was derived from a cross between two adapted clones. Populations 1 and 2 were produced from crosses involving a clone (ND860-2) that has some undesirable traits, such as very short dormancy, which were introgressed into adapted germplasm along with the cold-chipping ability from *Solanum phureja* (Ehlenfeldt et al. 1990). Certainly, to select clones low in reducing sugars from Population 3 would require more effort, but could also provide opportunity for making some progress for other important traits.

Because reducing sugars are negatively correlated with chip colour, positively-correlated responses to selection for chip quality would be expected in selecting for a reduced sugar content. The predicted correlated response estimates were positive, and were similar to the direct response estimates, suggesting that indirect selection for chip colour, based on selection for fructose and glucose, would give gains comparable to direct selection.

The higher predicted correlated responses to selection within environment can be explained by the fact that genetic variances and covariances estimated for the traits within environment included genotype × environment interactions.

Results of this study indicated that indirect selection, by either fructose or glucose content after cold storage, were as effective as direct selection for chip colour. Thus, both of the reducing sugars assessed after cold storage can be used in screening procedures for chip colour when breeding potatoes for processing.

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References

ap Rees T, Dixon WL, Pollock CJ, Frank F (1981) Low temperature sweetening of higher plants. In: Friend J, Rhodes MJC (eds) Recent advances in the biochemistry of fruits and vegetables. Academic Press, New York, pp 41–44

Barichello V, Yada RY, Coffin RH, Stanley DW (1990) Respiratory enzyme activity in low-temperature sweetening of susceptible and resistant potatoes. J Food Sci 55:1060–1063

Brown J, Mackay GR, Bain H, Griffith DW, Allison MJ (1990) The processing potential of tubers of the cultivated potato, *Solanum tuberosum* L., after storage at low temperatures. 2. Sugar concentration. Potato Res 33:219–227

Burton WG (1969) The sugar balance in some British potato varieties during storage. II. The effects of tuber age, previous storage temperature, and intermittent refrigeration upon low-temperature sweetening. Eur Potato J 12:81–95

Burton WG, Wilson AR (1978) The sugar content and sprout growth of tubers of potato cultivar Record, grown in different localities, when stored at 10, 2 and 20 °C. Potato Res 21:145–162

Chitsaz M (1983) Inheritance of factors affecting the quality of processed potatoes (*Solanum tuberosum* group *Tuberosum* L.). PhD thesis, North Dakota State University

Coffin RH, Yada RY, Parkin KL, Grodzinski B, Stanley DW (1987) Effect of low temperature storage on sugar concentrations and chip color of certain processing potato cultivars and selections. J Food Sci 52:639–645

Colon LT, Sijpkes L, Hartmans KJ (1989) The cold stability of *Solanum goniocalyx* and *S. phureja* can be transferred to adapted diploid and tetraploid *S. tuberosum* germplasm. In: Proc Conf EAPR-EUCARPIA. Parental line breeding and selection in potato breeding. Pudoc, Wageningen, The Netherlands, pp 76–80

Ehlenfeldt MK, Lopez-Portilla DF, Boe AA, Johansen RH (1990) Reducing sugar accumulation in progeny families of cold chipping potato clones. Am Potato J 67:83–91

Falconer DS (1989) Introduction to quantitative genetics, 3rd edn. Longman Scientific and Technical, New York

Federer WT, Raghavarao D (1975) On augmented designs. Biometrics 31:29–35

Grassert V, Vogel J, Bartel W (1984) Einfluss der sorte und einiger umweltfaktoren auf die neigung von kartoffelknollen zur zuckerbildung während einer mehrmonatigen lagerung bei 4 °C. Potato Res 27:365–372

Johansen RH (1987) Breeding of new potato chip varieties. Proc Natl Chipping Potato Seminar. Nashville, Tennesse, March 6

Leszkowiat MJ, Barichello V, Yada RY, Coffin R, Lougheed EC, Stanley DW (1990) Contribution of sucrose to nonenzymatic browning in potato chips. J Food Sci 55:281–284

Marquez G, Añon MC (1986) Influence of reducing sugars and amino acids in the color development of fried potatoes. J Food Sci 51:157–160

Schwimmer S, Benevue A, Weston WJ, Porter AL (1954) Potato composition: survey of major and minor sugar and starch components of the white potato. J Agric Food Chem 2:1284–1290

Shallenberger RS, Smith O, Treadway RH (1959) Role of the sugars in the browning reaction in potato chips. J Agric Food Chem 7:274–277

Simmonds NW (1979) Principles of crop improvement. Longman, London New York

Stevenson FJ, Akeley RV, McLean JG (1954) Potato utilization in relation to variety (heredity), and environment. Am Potato J 31:327–340

Tai GCC (1986) A method to construct confidence intervals for expected response to multi-trait selection. Theor Appl Genet 71: 595–599

Tai GCC (1989) A new procedure to construct confidence intervals for genotypic variance and expected response to selection. Génome 32:307–308

Talburt WF, Schwimmer S, Burr HK (1975) Structure and chemical composition of the potato tuber. In: Talburt WF, Smith O (eds) Potato processing. The AVI Publishing Co., Westport, Connecticut, pp 11–42

Webb RE, Wilson DR, Frank JA, Goth RW, Shumaker JR, Henninger MR (1984) Russette: a russet-skin potato variety, combining high quality, high yields, and adaptation to the northeastern states and Florida. Am Potato J. 61:77–81

Wilson AM, Work TM, Bushway AA, Bushway RJ (1981) HPLC determination of fructose, glucose, and sucrose in potatoes. J Food Sci 46:300–301