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Germplasm Release: Tetraploid Clones with Resistance to Cold-Induced Sweetening

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Abstract Long-term cold storage is necessary to supply potatoes to the processing industry throughout the year. Cold-induced sweetening prevents current potato cultivars from producing acceptable chips after cold storage. Resistance to cold-induced sweetening has been introgressed into the cultivated potato from wild *Solanum* relatives. This paper describes five tetraploid interspecific hybrid clones that can be used in breeding programs to improve chip quality in cold-stored tubers. The clones are male and female fertile, and are adapted to temperate zone production environments. All clones except M1 have low levels of glycoalkaloids. They produce acceptable chip color following storage at 4.4°C for 3 months. Tubers from all clones have high specific gravity. Following cold storage, tuber glucose and fructose contents are low compared to standard cultivars. Tuber sucrose contents for the five clones are either comparable to that in standard cultivars or much greater.

Resumen El almacenamiento en frío a largo plazo es necesario para proveer papas a la industria del procesamiento durante todo el año. El endulzamiento inducido por el frío evita que las variedades actuales de papa produzcan papas fritas aceptables después del almacenamiento en frío. La resistencia al endulzamiento por frío se ha introducido a la papa cultivada de parientes silvestres de *Solanum*. Este artículo describe cinco clones híbridos tetraploides interespecíficos que pueden usarse en programas de mejoramiento genético para mejorar la calidad de fritura en tubérculos almacenados en frío. Los clones son fértiles como macho o hembra, y se adaptan a ambientes de producción de zonas templadas. Todos los clones, excepto M1, tienen bajos niveles de glicoalcaloides. Producen color aceptable de hojuela después de un almacenamiento a 4.4°C por tres meses. Los tubérculos de todos los clones tienen alta gravedad específica. Después del almacenamiento en frío, los contenidos de glucosa y fructosa de los tubérculos son bajos comparados con las variedades estándar. El contenido de sacarosa del tubérculo en los cinco clones es comparable o mayor al de las variedades estándar.

Keywords Potato chip processing · *Solanum* · Wild germplasm · Low temperature sweetening · Reducing sugars

Introduction

Processing potatoes harvested in the fall in major production states are stored until they are needed at the processing plant (Hayes and Thill 2003). In 2008, 48% of the U.S. potato crop was used for the production of chips and fries (Anonymous 2009). Extending the storage season to make raw product available throughout the year decreases costs associated with shipping raw product and underutilization of processing facilities. Storage temperatures of 4–6°C increase long-term storage capabilities by minimizing losses due to rot, disease, and respiration (Sowokinos 2001). Cold storage temperatures also reduce winter heating costs and the need for chemical treatments in storage to control disease and sprouting. At cold storage temperatures, however, tubers accumulate undesirable levels of the reducing sugars fructose and glucose and are said to undergo cold-induced sweetening (CIS) (Blenkinsop et al. 2004; Denny and Thornton 1940;

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Gould et al. 1979). When tubers with high reducing sugars are used to make chips or fries, reducing sugars react with amino acids in a non-enzymatic Maillard reaction (Denny and Thornton 1941; Habib and Brown 1957) to produce fried products that are dark-colored, bitter-tasting and unattractive to consumers. Chipping potatoes are typically stored at 8–10°C (Blenkinsop et al. 2004) to minimize this problem, even though colder storage temperatures are desirable (Thill and Peloquin 1995).

The potato industry is interested in using conventional breeding to develop chipping cultivars with resistance to CIS (Hayes and Thill 2002; MacKay et al. 1990; Periera et al. 1994; Xiong et al. 2002). In a previous study, we described the use of wild *Solanum* species to develop adapted diploid clones having a high resistance to CIS (Hamernik et al. 2009). We have used sexual polyploidization to introgress that germplasm into tetraploid breeding clones, which we have evaluated over several years. This report describes fertility, agronomic traits, tuber glycoalkaloid content, and chip quality of five adapted tetraploid breeding clones with heritable, stable resistance to CIS.

Materials and Methods

Pedigrees of Clones

The tetraploid clones reported here are derived from diploid clones described previously (Hamernik et al. 2009). All five clones contain the haploid-wild species hybrid clone US-W973 x *S. chacoense* (chc), named HC (Fig. 1). The haploid US-W973 was derived from the Wisconsin advanced selection Wis Ag 231. In a previous study, HC produced the highest proportion of offspring with resistance to CIS (Hamernik et al. 2009). *Solanum raphanifolium* (rap) is also a good source of resistance to CIS (Hamernik et al. 2009; McCann et al. 2010) and it is in the pedigrees of all five clones. White Pearl contains resistance to CIS (Groza et al. 2006) and makes up 50% of the germplasm of clone M5. Clones M2 and M3 are full sibs. All clones were developed by unilateral sexual polyploidization in which the diploid female parent produced 2n eggs and the tetraploid male parent produced n pollen. After sexual polyploidization, clones M4 and M5 underwent additional crosses to the tetraploid clones W870 (M4) and W1005 (M4 and M5). Clones W870, W1005, W1242, and W1351 are tetraploid parents from the Wisconsin breeding program.

Fertility Evaluations

Greenhouse-grown plants were used for fertility evaluations. To evaluate female fertility, flowers were emasculated before anthers dehisced and bulked pollen from standard cultivars (Atlantic, Langlade, Kennebec, Superior, Ranger Russet, and White Pearl) was applied to stigmas. Fruits were retained on plants for 3 weeks after pollination, removed and stored at room temperature for 3 weeks. Seeds were then extracted and plump seeds counted. Male fertility was measured in a similar way, except that pollen from test clones was applied to the stigmas of the cultivars. Pollen viability was also scored based on the number of plump, stained pollen grains observed after treating with acetocarmine solution (1%) (Marks 1954).

Field Trials

Tubers for chip, sugar, and specific gravity evaluations were produced using standard production practices at the Lelah Starks Agricultural Experiment Station near Rhinelander, Wisconsin, from 2002 through 2009. Seed tubers were planted in late April or early May and tubers were harvested with a single-row digger in early September, 2 weeks after vine kill. Tubers were placed directly into cold storage without preconditioning. Tubers were stored at 4.4°C for 3 months and then chipped directly or reconditioned for 2 weeks at room temperature (23°C). The clones were entered into a yield trial in 2008 at the Hancock, Wisconsin, Agricultural Experiment Station. Three replications of five-hill units were planted in a randomized complete block design on May 5 and harvested on September 9, 2 weeks after vine kill. Plots were harvested with a single row digger and tubers with a diameter larger than 4 cm were picked up by hand, combined and weighed in the field. Those that were smaller than 4 cm fell through the digger chain and were not picked up.

On May 4 and May 6, 2010, 15-hill plots of the five clones and the cultivars Atlantic, Snowden, and White Pearl were planted at the Hancock and Rhinelander Agricultural Research Stations, respectively. They were scored three times during the summer for maturity and vigor. Maturity was evaluated as 0 - dead, 1 - mostly dead vines, 2 - yellow, prostrate vines, 3 - some flowers, vines erect, 4 - full flower, 5 - pre-flower. Vigor was evaluated as 5 – very large plants, 4 – vine size of a vigorous cultivar, 3 - vine size of a small cultivar, 2 – smaller than a cultivar, 1 – less than 30 cm in size. Scoring dates were July 6, July 21, and August 9 at Rhinelander and July 21, August 3, and August 18 at Hancock.

Specific gravity of field grown tubers was determined using 3.5 kg samples collected from Hancock in 2007–2009. Tubers were weighed in water and in air. Specific gravity was calculated as weight in air (weight in air - weight in water)$^{-1}$.

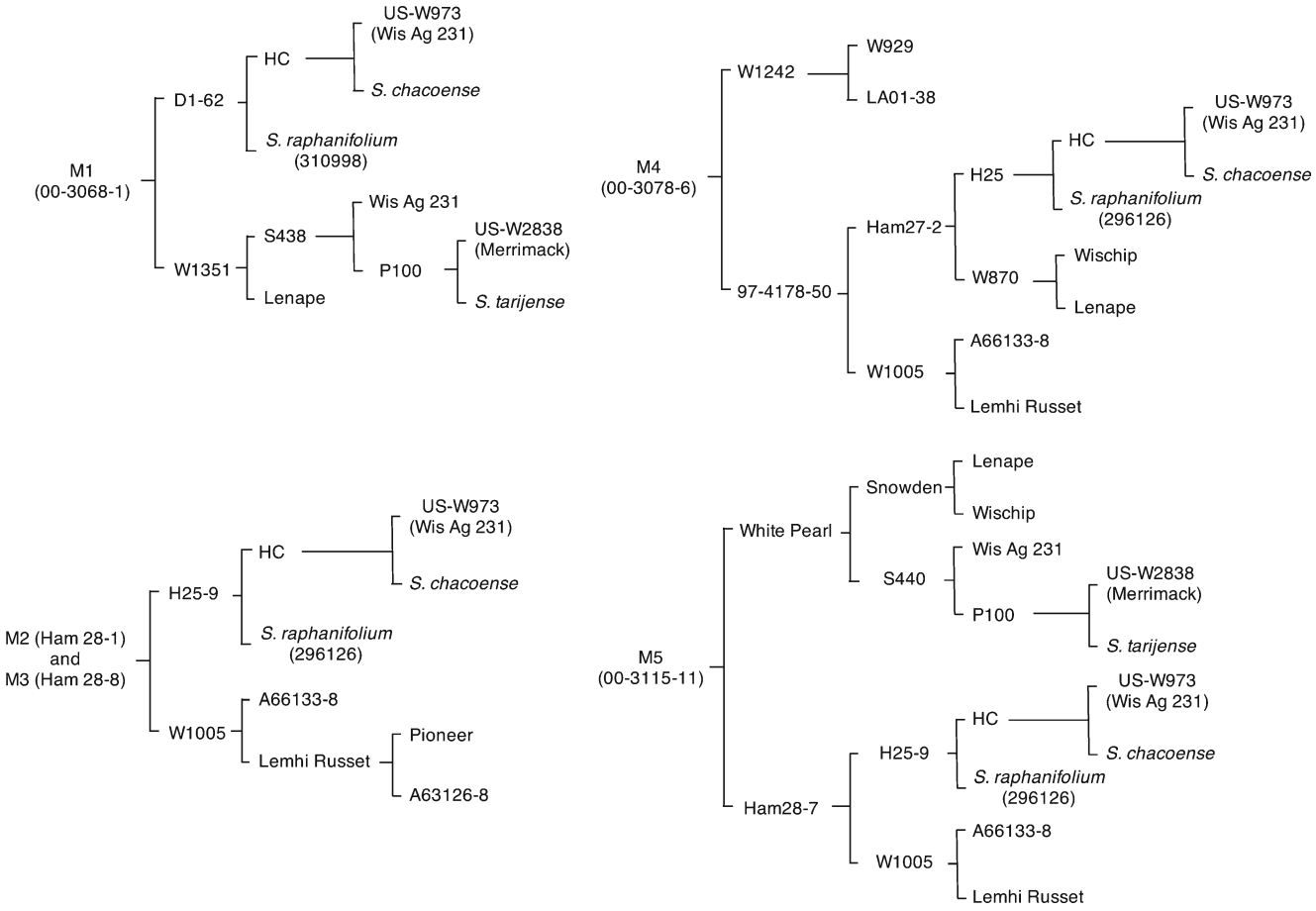

Fig. 1 Pedigrees of clones M1, M2/M3, M4 and M5. *Solanum tarijense* has been re-named *S. berthaultii*

Glycoalkaloids

Two tuber samples from the 2009 Rhinelander field plot were peeled and lyophilized after harvest. Alpha-solanine and alpha-chaconine were quantified by reverse-phase liquid chromatography (RP-LC). Approximately 2 g of powdered, lyophilized sample was added to an acidified ion pairing solution (0.02 M 1-heptanesulfonic acid sodium salt, monohydrate in 2% (v/v) acetic acid) and extracted for 3 min with a Polytron tissue homogenizer. The resulting

Table 1 Maturity, yield and specific gravity of tetraploid breeding lines and cultivars grown at Hancock, WI. Vine maturity scores were collected on three dates in 2010. Yield data are based on a replicated field trial in 2008. Specific gravity data are averaged across 3 years (2007–2009)

Clone	Vine maturity[a]			Yield[b]	Specific Gravity
	07/21/10	08/03/10	08/18/10		
M1	3.0	3.0	3.0	1.01±0.17	1.094±0.002
M2	3.0	3.0	3.0	1.08±0.20	1.100±0.006
M3	2.0	2.0	2.0	1.31±0.23	1.093±0.008
M4	2.0	2.0	2.0	–	1.084±0.003
M5	2.0	2.0	2.0	1.68±0.05	1.078±0.003
Atlantic	2.5	2.5	2.5	2.24±0.11	1.086±0.001
Snowden	3.0	3.0	2.5	2.77±0.23	1.083±0.004
White Pearl	3.0	2.5	2.5	1.93±0.35	1.081±0.007

[a] 0 - dead, 1 - mostly dead vines, 2 - yellowing, prostrate vines, 3 - some flowers, vines erect, 4 - full flower, 5 - pre-flower

[b] kg/hill

extract was centrifuged to pellet tissue debris and a 10 mL aliquot of the supernatant was passed through a methanol-activated tC-18 SPE (Waters Corp, Milford, MA, Cat # WAT036810) cartridge followed by an acetonitrile-water (20:80, v/v) wash. After vacuum drying, the sample was eluted from the cartridge with a tetrahydrofuran-water-acetonitrile (50:30:20, v/v) solution and 20 µl was injected into the LC system, equipped with a diode array detector (DAD) for analysis. Separation was accomplished on a C-6 analytical column, with a buffered (pH 3.5) mobile phase.

Chip Scores

A 1–2 mm thick, longitudinal slice from the center of the tuber was rinsed in tap water and fried in corn oil at 190°C until bubbling ceased. Each chip was scored visually for color using a scale of 1.0 to 10.0 (light to dark), at 0.5 intervals, based on the Snack Food Association (Arlington, VA) color standards reference chart for potato chips. Chips with a color score of 4.5 or less were considered acceptable (Hamernik et al. 2009).

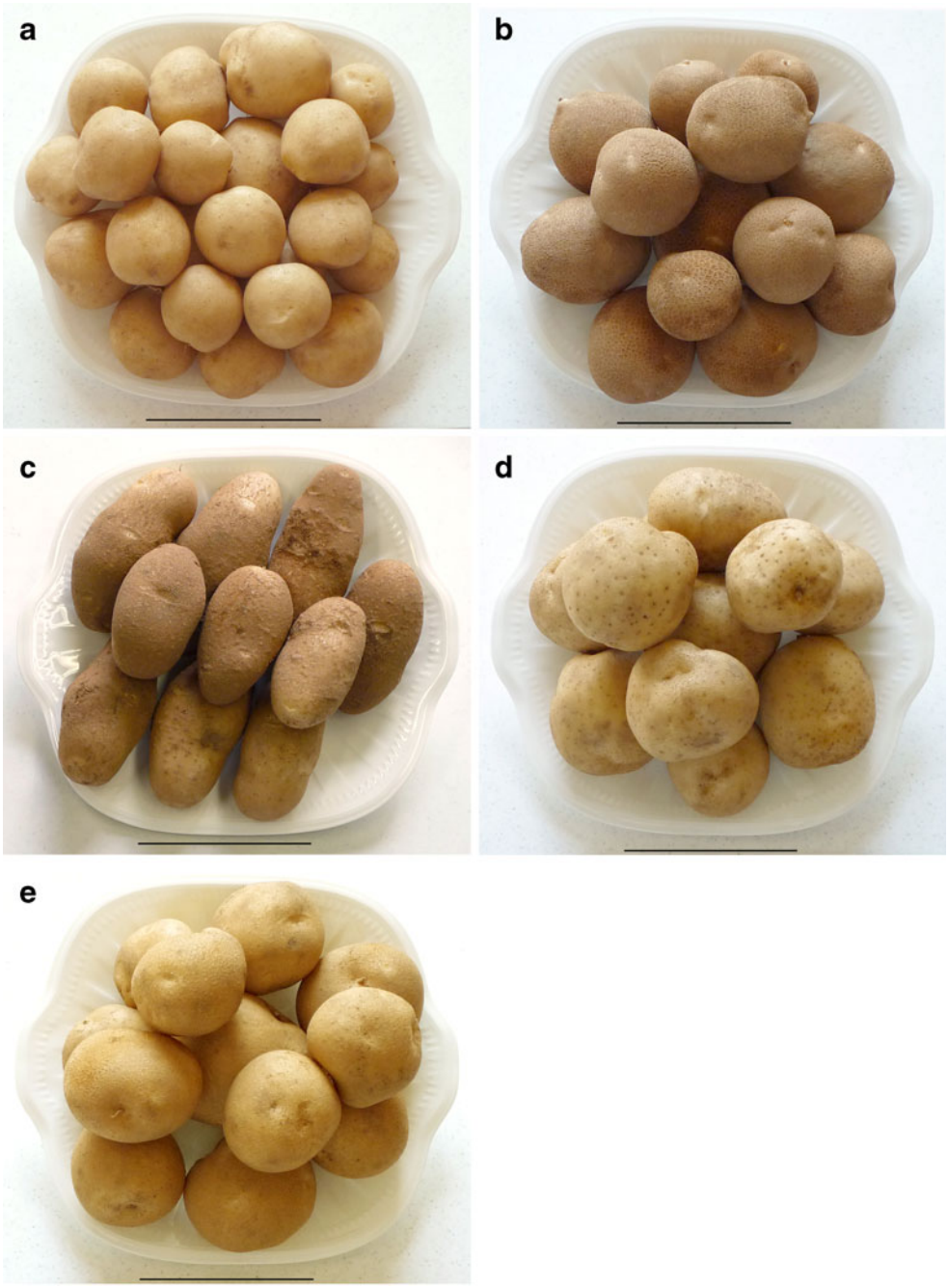

Fig. 2 Photos of tubers of M1 (**a**), M2 (**b**), M3 (**c**), M4 (**d**), and M5 (**e**). Bar indicates 10 cm

Table 2 Male and female fertility of tetraploid breeding lines

Clone	Female Fertility			Male Fertility			
	P[a]	S[b]	S/P	P	S	S/P	% Stained[c]
M1	15	860	57	29	90	3	20–50
M2	55	6488	118	46	1390	30	60–80
M3	22	3626	165	29	4171	144	50–80
M4	33	1120	34	96	2612	27	70–80
M5	7	48	7	27	635	24	60–70

[a] Number of pollinations

[b] Number of plump seeds

[c] Percent pollen grains stained with acetocarmine

Sugar Evaluations

After removing slices for chipping, remaining tuber pieces were frozen in liquid nitrogen, stored at −80°C, and lyophilized. Freeze-dried samples were ground to a fine powder with a mortar and pestle and approximately 0.15 g dry powder used for HPLC analysis as described in Bethke and Busse (2008) using a column temperature of 20°C.

Flavor Evaluations

In February, 2010, after 5 months in storage at 7.2°C, tubers were reconditioned at room temperature for 1 week. Chips were prepared by frying slices at 190°C in vegetable oil until bubbling ceased, and then salted with 1 g salt per 100 g chips. The next day, a taste panel was carried out using 15 panelists. Each panelist received two plates, each containing three chips from four samples. Samples were arranged in random order on the plate and coded with random three-digit numbers. The arrangement of samples on the plate was the same for all panel members. Scoring was carried out by placing a mark along a 135 mm horizontal line on a score sheet. The position of the mark on the line represented the panelists' assessment of oiliness (not oily to very oily), potato flavor intensity (little potato flavor to distinct potato flavor), off-flavor (no off-flavor to distinct off-flavor) and overall acceptability (unacceptable to very acceptable). The first three criteria are objective, while the last is subjective. The distance from the beginning of the score line to the panelist's mark (in mm) constituted the primary data set that was used for quantitative analysis. The first plate contained M1, M4, and M5, along with White Pearl. The second plate contained M2, M3, another chip selection, and White Pearl.

Data Analysis

All data were analyzed using PROC GLM in SAS. Since the specific gravity, chip score, and sugar analysis data were not derived from replicated trials, years were considered to be replications in the ANOVA. Means separations were carried out using a protected Least Significant Difference test at $P=0.05$.

Results and Discussion

The selected clones have been grown in the field and evaluated for resistance to CIS for 8 years (Supplementary Tables 1–4). Vine appearance of the five clones grown in the field was similar to that of standard cultivars. At both Hancock and Rhinelander, all clones except M2 were given vigor scores of four, as were the cultivar standards. M2 was slightly less vigorous, with a score of 3.5. Clones M1 and M2 are similar in maturity to Snowden, while M3, M4 and M5 were slightly earlier, with maturity scores similar to those of Atlantic (Table 1).

When grown in the field, all five breeding lines produce smooth tubers. M1 is a round white clone with high tuber set and relatively small tubers. M2 is a round russet clone and its full-sib, M3, is a long russet clone. M4 is a round white clone with smooth skin and medium size and set. M5 is a round white clone with buff skin and medium size and set. Photographs of representative tubers from each clone are shown in Fig. 2.

All clones produced adequate flowers for breeding and have been characterized for fertility attributes (Table 2). When used as females, seed set ranged from 7 to 165 seeds per pollination. Based on stainability with acetocarmine as a marker for viability, all clones are moderately to highly male fertile. The lowest fertility was recorded in M1, with pollen staining ranging from 20 to 50%, which was

Table 3 Solanine, chaconine, and total glycoalkaloid content of tetraploid breeding lines

Clone	Solanine (mg g^{-1} DW)	Chaconine (mg g^{-1} DW)	Total (mg g^{-1} DW)	Total (mg 100 g^{-1} FW)
M1	0.975±0.120	0.985±0.106	1.960±0.226	47.4
M2	0.061±0.004	0.103±0.021	0.164±0.018	4.1
M3	0.039±0.006	0.052±0.020	0.091±0.012	2.2
M4	0.028±0.004	0.100±0.037	0.127±0.034	2.9
M5	0.196±0.037	0.289±0.055	0.485±0.091	9.9

Table 4 Direct and reconditioned chip scores of tetraploid breeding lines and cultivars, averaged over four production years (2006–2009). Tubers were stored at 4.4°C for 3 months and chipped directly out of cold storage or reconditioned for 2 weeks at room temperature

Clone	Direct	Reconditioned
M1	4.1±0.8a	4.1±1.0a
M2	5.3±1.0ab	4.3±0.3a
M3	5.0±1.2abc	4.4±1.3a
M4	6.4±1.1bcd	3.8±0.5a
M5	6.3±1.0 cd	4.6±0.8a
Atlantic	9.0±0.0e	6.0±0.9b
Snowden	9.0±0.0e	4.0±0.0a
White Pearl	7.5±0.5d	3.9±0.6a

Data are means ± standard deviations. Within a column, numbers followed by different letters are different at $P=0.05$

reflected in a low seed set when used as a male parent. All other clones exhibited at least 50% pollen viability based on staining with acetocarmine. When used as males, seed set ranged from 3 to 144 seeds per pollination (Table 2).

Specific gravity is very high in all selected clones (Table 1). Clone M2 is exceptionally high in solids, with specific gravity across years averaging 1.100. In contrast, tubers from the chip cultivar Atlantic grown under the same conditions had a specific gravity of 1.086. Tuber yields from the selected clones were lower than from standard cultivars (Table 1), but all clones are adapted to temperate zone production environments and readily set tubers in all years. The lowest yielding clones (M1 and M2) contain the highest proportion of wild species germplasm (Fig. 1).

One concern with the use of wild *Solanum* relatives in breeding is that they may contain high levels of toxic glycoalkaloids (Hall 1992). The major glycoalkaloids in potato are α-solanine and α-chaconine and the total glycoalkaloid threshold considered safe for human consumption is 20 mg/100 g fresh weight (Sinden and Webb 1974). In all five clones, α-chaconine content was higher than α-solanine content (Table 3) and all clones except for M1 had total glycoalkaloid contents that were well below the threshold for safe consumption. At 47 mg 100 g^{-1} FW, tubers from clone M1 contained approximately 2.5 times the acceptable amount of total glycoalkaloids. These clones are being released for use as parents, however, and glycoalkaloids in the offspring are likely to be lower than in the parents (Sanford et al. 1996). As a precaution, however, it will be necessary to monitor tuber glycoalkaloids in progeny, especially in offspring from M1.

The clones with the highest proportion of wild germplasm (M1, M2, and M3) produced the lightest colored chips directly out of cold storage. Clones M1–M5 contain 44%, 38%, 38%, 9%, and 25% wild germplasm, respectively. The correlation between chip score at 4.4°C and percent wild germplasm is −0.85 ($P<0.0001$). There was a significant effect of clone ($P<0.0001$) but not year ($P=0.7559$) for chip color when tubers were fried directly from storage at 4.4°C. Clone M1 had the lowest mean chip color (4.1), while M4 was the highest with a score of 6.4 (Table 4). In contrast, mean chip color scores for Atlantic, Snowden, and White Pearl were 9.0, 9.0, and 7.5, respectively. Direct chip scores for all five germplasm lines were significantly lower than Atlantic and Snowden. All clones and standard cultivars responded to reconditioning and produced chips with lighter color than those fried directly out of cold storage (Table 4). Again, there was a

Table 5 Glucose, fructose, and sucrose content (mg g^{-1} DW) in tubers of tetraploid breeding lines and cultivars averaged across three production years (2006–2008). Tubers were stored at 4.4°C for 3 months and chipped directly out of cold storage or reconditioned for 2 weeks at room temperature

Clone	Direct			Reconditioned		
	Glucose	Fructose	Sucrose	Glucose	Fructose	Sucrose
M1	0.66±0.62a	1.52±0.97a	5.70±3.48a	0.59±0.50ab	1.21±1.26a	4.93±1.32a
M2	1.56±0.82abc	2.15±0.89ab	33.98±13.07d	0.41±0.24a	0.53±0.36a	13.15±6.11b
M3	0.88±0.24ab	1.52±1.27a	19.41±11.60c	0.37±0.26a	0.62±0.61a	8.26±2.55ab
M4	1.49±1.68abc	2.40±1.59ab	16.46±10.98bc	0.17±0.10a	0.31±.029a	7.34±.049a
M5	1.63±0.66abc	2.92±0.76abc	10.82±7.28abc	0.26±0.07a	0.65±0.52a	3.62±2.37a
Atlantic	5.31±3.52c	7.28±2.80bc	18.11±9.84c	1.31±0.47b	2.66±0.50b	4.31[a]
Snowden	4.92±4.01bc	7.77±5.40c	13.09±5.37abc	0.21±0.05a	0.37±0.18a	6.35±0.31a
Superior	13.19±3.94d	19.53±4.78d	14.70±7.95abc	3.17±1.51c	10.37±1.51c	4.92±0.95a
White Pearl	3.63±3.35abc	5.42±4.25abc	8.00±2.73ab	0.27±0.07a	0.53±0.14a	5.61±1.23a

[a] Data only available for 1 year (2008)

Data are means ± standard deviations. Within a column, numbers followed by different letters are different at $P=0.05$

significant effect of clone (P=0.0066), but not year (P=0.1151) for chip color following reconditioning. Clone M4 had the lightest chips (3.8), while the darkest after reconditioning were from M3 (4.4). Cultivar means were 6.0, 4.0, and 3.9 for Atlantic, Snowden, and White Pearl, respectively. All germplasm lines had lighter chips than Atlantic, but not Snowden or White Pearl.

Taste panelists did not detect differences among the chip samples for any of the evaluation criteria (P=0.05). It is interesting that taste panelists were not able to detect bitterness in M1, since that clone had higher glycoalkaloid levels than the other breeding lines. Taste panelists have been reported to be able to taste bitterness when glycoalkaloid levels are above 14 mg 100 g^{-1} fresh tuber weight (Sinden et al. 1976). A significant positive correlation (r=0.26) was detected between chip flavor intensity and overall acceptability (P=0.0035), and a significant negative correlation (r=−0.43) was detected between off-flavor and overall acceptability (P<0.0001).

In tubers sampled directly out of cold storage, differences among clones were significant for glucose, fructose, and sucrose levels (P=0.0009, 0.0003, and 0.0005, respectively). Mean glucose and fructose levels were lower than the cultivar standards (Table 5). The effect of year was not significant for glucose and fructose (P=0.0752 and 0.2417), but sucrose levels varied across years (P=0.0003). Sucrose content in tubers of selected clones stored for 3 months at 4.4°C ranged from 5.70 (M1) to 33.98 (M2) mg g^{-1} dry weight, with clone M2 having a higher sucrose content than the other breeding lines and cultivars (Table 5). Despite the high sucrose level, this clone had average glucose and fructose contents that were less than those found in the cultivars and comparable to those in the other breeding lines. A similar trend was seen in reconditioned tubers. In comparison with previously characterized clones of *S. raphanifolium* and interspecies-hybrids with HC (Bhaskar et al. 2010), these data suggest that M2 may have very low amounts of vacuolar invertase activity.

Availability

The five clones described in this paper are available as tissue culture plantlets from the US Potato Genebank, Sturgeon Bay, Wisconsin. They may be used for research purposes and for the development and commercialization of new cultivars.

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Disclaimer Reported use of brand name products does not imply an endorsement by the USDA.

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