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## Effects of Temperature and Low Oxygen Atmospheres on Respiration, Chip Color, Sugars, and Malate of Stored Potatoes<sup>1</sup>

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**Abstract.** Following curing and a period of storage at 10°C, potato (*Solanum tuberosum* L.) tubers were stored for 4 to 5 weeks at 1° or 10° in controlled atmospheres consisting of either air, 2.5% O<sub>2</sub> (balance N<sub>2</sub>), or N<sub>2</sub>. CO<sub>2</sub> production of tubers stored in air at 10° was relatively constant. When tubers were stored in air at 1°, CO<sub>2</sub> production initially was lower than at 10° in air. It then increased to a maximum after about 15 days and eventually declined again. Storage in 2.5% O<sub>2</sub> or N<sub>2</sub> prevented the increase in CO<sub>2</sub> production that occurred after several days of storage in air at 1°. Malate and citrate were the only organic acids detected in significant amounts in juice extracted from tubers when experiments were terminated. Changes in citrate showed no consistent trends. Tubers stored in air at 1° had higher sucrose, fructose, glucose, and malate levels than tubers stored at 10°. Storage in N<sub>2</sub> at 1° prevented the malate, sucrose, and reducing sugar increases. Storage in 2.5% O<sub>2</sub> inhibited the malate, fructose, and glucose increases at 1° and reduced the sucrose content of 'Monona' and 'Norchip' cultivars, which accumulated large amounts of sucrose during storage in air at 1°. Sucrose content of 'Kennebec' was not affected by 2.5% O<sub>2</sub>. Storage in 2.5% O<sub>2</sub> slowed the accumulation of fructose and glucose, but only 'Monona' and 'Norchip' yielded acceptable chips after storage in 2.5% O<sub>2</sub> at 1°. All 3 cultivars yielded acceptably colored chips after storage in N<sub>2</sub> at 1°, but the development of blackheart when tubers were returned to air makes N<sub>2</sub> an unacceptable storage atmosphere at this temperature. Storage in N<sub>2</sub> resulted in soft rot at 10°.

Potatoes intended for chipping are commonly stored at or above 10°C. This avoids the unacceptably dark chip color caused by reducing sugar accumulation at lower temperatures (21), but increases the losses from sprouting and decay. Lower storage temperatures may be possible with the use of controlled atmospheres, but results from research with potatoes have been variable (8, 12).

The biochemical mechanism of chilling-induced sweetening

in potato tubers is not conclusively established. Pollock and ap Rees (14) suggested that the cold lability of key glycolytic enzymes resulted in low temperature inhibition of glycolysis with consequent accumulation of hexose phosphates and then sucrose synthesis. Dixon and ap Rees (4) stressed the role of phosphofructokinase and pyruvate kinase in this respect. Isherwood (10) found that hexose phosphates and other phosphate esters increased within the first 2 days of chilling, but that sucrose and reducing sugars did not accumulate until after more than 10 days of chilling. In an earlier study, Isherwood (9) concluded from an examination of ATP equivalents that the increased respiration which accompanied chilling was quantitatively related to the conversion of starch to sugar. In addition, the ATP equivalent of the extra CO<sub>2</sub> output was similar to that predicted from known biochemical pathways linking starch and sugar.

Of the known respiratory pathways, only glycolysis continues to function under anaerobic conditions. We attempted to exploit the hypothesized cold lability of glycolytic enzymes by investigating the respiration of stored potatoes in response to combinations of low O<sub>2</sub> atmospheres and temperature. We also

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determined the effects of these atmosphere and temperature treatments on chip color and sucrose, glucose, fructose, and malate levels of several cultivars.

### Materials and Methods

Potato tubers for these experiments were grown on a Howard gravelly loam at the Homer C. Thompson Vegetable Research Farm, Freeville, N.Y. Fertilization, pest control, and other cultural practices conformed to standard recommendations for up-state New York. In late September, tubers were harvested, washed, and graded. Following curing, tubers were stored at 10°C until needed. No sprout inhibitors were applied. 'Monona' and 'Norchip' tubers harvested in September 1977, were used in the first experiment during February 1978. The 2nd experiment, during November 1978, utilized 'Monona', 'Norchip', and 'Kennebec' tubers harvested in September 1978.

Treatments were a complete factorial of cultivars, temperatures (10° and 1°C), and atmospheres (air, 2.5% O<sub>2</sub>, and N<sub>2</sub>), arranged in a split-plot design with temperatures as the main plot (6). There were 3 replications of 15 tubers each. In preparation for storage experiments, tubers were washed in a dilute (0.01%) sodium hypochlorite solution and allowed to dry. Samples were then weighed and placed in clean 20-l containers. The containers were sealed and the appropriate humidified gas mixture was passed over the potatoes via a flow-through system. Gas mixtures were made from compressed air and nitrogen. Flow rates were established with capillary tubing and effluent flow rates were determined with a bubble flow-meter. Effluent flow rates for air were about 8 and 4 liters hr<sup>-1</sup> at 10° and 1°, respectively. Flow rates for 2.5% O<sub>2</sub> and N<sub>2</sub> treatments were about half the rates for air treatments. CO<sub>2</sub> levels around the samples never exceeded 0.3%.

Respiration was monitored with a Fisher Model 1200 Gas Partitioner and a Hewlett Packard 3380A integrator. Calibration was with known standards (CO<sub>2</sub> and O<sub>2</sub>) purchased from Matheson Gas Products. Respiration data were analyzed as a split-split plot with time as the main plot, temperature as the subplot, and cultivars and atmospheres as sub-subplots.

Tubers were made into chips and assayed for sugars and organic acids after 33 and 30 days in the first and second experiments, respectively. Procedures for chipping, juice extraction, and sugar analyses were those reported by Ewing et al. (5).

Table.1 Effect of cultivar, storage temperature, and atmosphere on the respiration of 'Kennebec', 'Monona', and 'Norchip' tubers in experiment 2.

Storage temp (°C)	Respiration (mg CO <sub>2</sub> kg <sup>-1</sup> hr <sup>-1</sup> )			
	Atmosphere	Kennebec	Monona	Norchip
10	Air	2.5e <sup>c</sup>	2.0f	2.6e
1	Air	3.0d	3.4c	4.0b
10	2.5% O <sub>2</sub>	1.8fg	1.6fg	1.8fg
1	2.5% O <sub>2</sub>	1.7fg	1.3g	1.5g
10	N <sub>2</sub>	3.9b	4.4a	3.8b
1	N <sub>2</sub>	0.9h	0.7h	0.8h

<sup>a</sup>Mean separation of the 18 values by Duncan's multiple range test, 5% level.

Potato extracts were analyzed for organic acids as described earlier (18). A separate analysis of variance was conducted for each variable in both experiments.

### Results

**Respiration.** In the first experiment, there was a significant (5% level) cultivar × storage temperature interaction. When stored at 10°C, 'Norchip' had a significantly higher respiration rate than 'Monona' (3.7 and 2.5 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> for 'Norchip' and 'Monona', respectively). When stored at 1°, the cultivar difference was not as great (2.3 and 1.7 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> for 'Norchip' and 'Monona', respectively). There was also a significant (0.01% level) cultivar × atmosphere interaction in the first experiment. When stored in air, 'Norchip' had a significantly higher respiratory rate than 'Monona' (4.5 and 2.7 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup>, respectively). Storage in either 2.5% O<sub>2</sub> or N<sub>2</sub> greatly diminished the respiratory differences between cultivars (2.0 and 2.5 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> for 'Norchip' and 1.7 and 1.9 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> for 'Monona' in 2.5% O<sub>2</sub> and N<sub>2</sub>, respectively).

In the second experiment, there was a significant (0.01% level) cultivar × storage temperature × atmosphere interaction

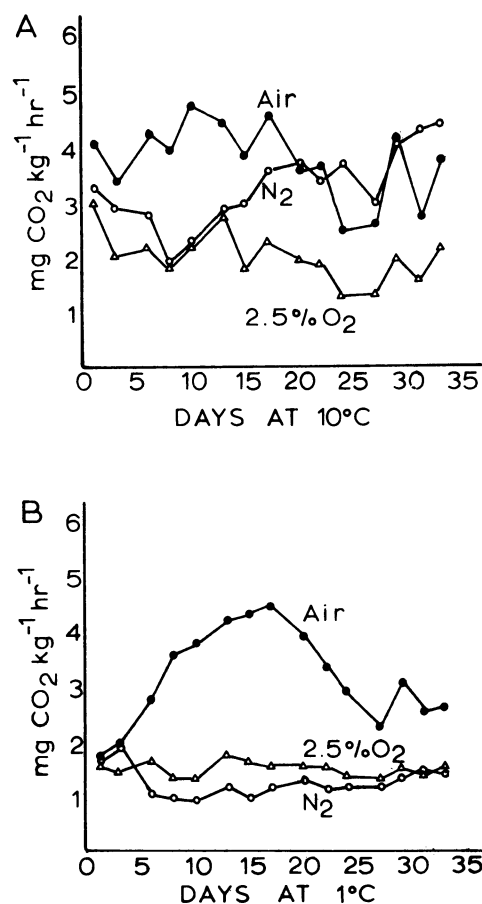


Fig. 1. Effect of controlled atmospheres on the CO<sub>2</sub> production of 'Monona' and 'Norchip' tubers stored at 10°C (A) and 1°C (B). The time × temperature × atmosphere interaction was only significant at the 8% level but is presented for comparison to Fig. 2. Data are combined for cultivars.

(Table 1). When stored in air, all 3 cultivars had a higher overall respiratory rate at 1° than at 10°C, although 'Kennebec' was not as affected as 'Monona' and 'Norchip'. In contrast, when stored in N<sub>2</sub> all 3 cultivars had a higher overall respiratory rate at 10°. When stored at 2.5% O<sub>2</sub>, there were no significant differences among cultivars and storage temperatures. In both experiments cultivar interactions with storage temperature and atmosphere treatments were due to differences in magnitude, not the direction of the response to the treatment.

There was a time × temperature × atmosphere interaction in both experiments (Fig. 1 and 2). At 10° C in air, the CO<sub>2</sub> production fluctuated around 4 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> in the first experiment (Fig. 1A) and was essentially steady near 2.5 mg CO<sub>2</sub> kg<sup>-1</sup> hr<sup>-1</sup> in the second experiment (Fig. 2A). CO<sub>2</sub> output during storage in air at 1° was initially lower than at 10°, but then increased to a peak level before gradually declining. Tubers stored in 2.5% O<sub>2</sub> had low levels of CO<sub>2</sub> output at both temperatures. At 10°, storage in N<sub>2</sub> depressed CO<sub>2</sub> output for 8 to 10 days; after that time, CO<sub>2</sub> production increased until the

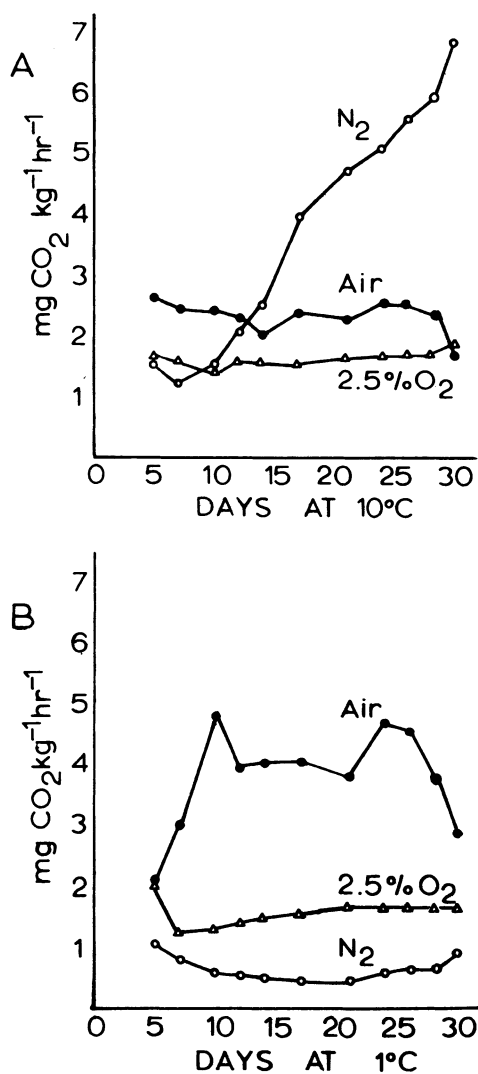


Fig. 2. Effect of controlled atmospheres on the CO<sub>2</sub> production of 'Monona', 'Norchip', and 'Kennebec' tubers stored at 10°C (A) and 1° (B). The time × temperature × atmosphere interaction was significant at the 0.01% level. Data are combined for cultivars.

Table 2. Main effect of cultivar on chip color and sucrose, fructose, and glucose content of 'Monona' and 'Norchip' tubers in experiment 1. Data are combined for temperatures and atmospheres.

Cultivar	Chip color (% reflectance <sup>2</sup> )	Sucrose (mM)	Fructose (mM)	Glucose (mM)
Monona	69***	16.6*	5.3*	6.5*
Norchip	56	32.3	9.4	14.1

<sup>2</sup>Crushed chips measured on Agtron Reflectance Meter M-400-A, calibrated with discs 5005 and 5052.5 for 0 and 100 readings, respectively. \*\*\*Significant at 5% (\*) or 0.1% (\*\*\*) by F test.

experiments were terminated. The tremendous increase in CO<sub>2</sub> production during storage in N<sub>2</sub> at 10° in the second experiment (Fig. 2A) may be attributable largely to the effect of soft rot development. In contrast to the 10° N<sub>2</sub> treatment, storage in N<sub>2</sub> at 1° reduced CO<sub>2</sub> production (Fig. 1 and 2).

**Chip color and sugars.** 'Monona' tubers produced significantly lighter chips and had significantly lower sucrose, fructose, and glucose levels than 'Norchip' tubers in experiment 1 (Table 2). Tubers stored in air at 1°C had a poor finished chip color and high levels of sucrose, glucose, and fructose (Table 3). Storage in 2.5% O<sub>2</sub> and N<sub>2</sub> at 1° resulted in a much improved chip color and reduced the sucrose, fructose, and glucose accumulation, compared to storage in air at 1°.

Tubers stored in N<sub>2</sub> developed a pink internal discoloration that tended to turn black when tubers were exposed to air after removal from storage (20). The disorder was more common at 10°C (100% and 54% affected at 10° and 1°, respectively). Only tubers stored in N<sub>2</sub> had this internal discoloration. When fried immediately after removal from storage, this discoloration only had a slight effect on chip color. Storage in N<sub>2</sub> at 10° also led to the development of soft rot decay in 33% of the tubers.

In the second experiment, 'Monona' and 'Kennebec' tubers produced the lightest and darkest chips, respectively. Storage in low O<sub>2</sub> atmospheres (2.5% O<sub>2</sub> and N<sub>2</sub>) improved the chip color

Table 3. Effect of storage temperature and atmosphere on the chip color and sucrose, fructose, and glucose content of 'Monona' and 'Norchip' tubers in experiment 1. Data are combined for cultivars.

Storage temp (°C)	Atmosphere	Chip color (% reflectance <sup>2</sup> )	Sucrose (mM)	Fructose (mM)	Glucose (mM)
10	Air	86 <sup>y</sup>	3.5 <sup>x</sup>	0.2 <sup>x</sup>	1.2 <sup>x</sup>
1	Air	16	99.6	33.8	41.2
10	2.5% O <sub>2</sub>	87	3.0	0.5	1.6
1	2.5% O <sub>2</sub>	55	30.6	5.3	7.5
10	N <sub>2</sub>	62	2.3	1.8	3.7
1	N <sub>2</sub>	68	7.8	2.1	6.7

<sup>2</sup>Crushed chips measured on Agtron Reflectance Meter M-400-A, calibrated with discs 5005 and 5052.5 for 0 and 100 readings, respectively.

<sup>y</sup>Orthogonal comparisons for the interactions of temperature × (air vs. [2.5% O<sub>2</sub> + N<sub>2</sub>]) and temperature × (2.5% O<sub>2</sub> vs. N<sub>2</sub>) were significant at P=0.001.

<sup>x</sup>Orthogonal comparison for the interaction of temperature × (air vs. [2.5% O<sub>2</sub> + N<sub>2</sub>]) was significant at P=0.001.

Table 4. Effect of cultivar, storage temperature, and atmosphere on the chip color and sucrose, fructose, and glucose content of 'Kennebec' (Ken), 'Monona' (Mon), and 'Norchip' (Nor) tubers in experiment 2.

Storage temp (°C)	Atmosphere	Chip color (% reflectance <sup>z</sup> )			Sucrose (mm)			Fructose (mm)			Glucose (mm)		
		Ken	Mon	Nor	Ken	Mon	Nor	Ken	Mon	Nor	Ken	Mon	Nor
10	Air	79bcd <sup>y</sup>	91a	84abc	3.9d	3.2d	5.7d	2.1d	0.7d	1.4d	4.2d	1.0d	1.8d
1	Air	11g	38f	33f	19.9cd	62.5b	90.3a	66.6a	15.4c	11.6c	77.3a	18.8c	25.1bc
10	2.5% O <sub>2</sub>	80bcd	92a	86ab	4.4d	4.3d	4.5d	2.5d	0.6d	0.7d	4.5d	0.8d	1.5d
1	2.5% O <sub>2</sub>	33f	69de	62e	18.4cd	19.8cd	29.6bc	23.2b	3.5d	4.5d	27.4b	4.0d	5.7d
10	N <sub>2</sub>	--- <sup>x</sup>	---	---	---	---	---	---	---	---	---	---	---
1	N <sub>2</sub>	72cde	91a	73bcde	3.9d	4.1d	4.4d	3.2d	0.5d	2.0d	4.5d	0.8d	2.6d

<sup>z</sup>Crushed chips measured on Agron Reflectance Meter M-400-A, calibrated with discs 5005 and 5052.5 for 0 and 100 readings, respectively.

<sup>y</sup>Mean separation of the 15 values within a dependent variable by Duncan's multiple range test, 5% level.

<sup>x</sup>All 10° N<sub>2</sub> treatments lost due to soft rot decay.

of potatoes stored at 1°C (Table 4). All of the tubers stored in N<sub>2</sub> at 10° rotted. Tubers stored in N<sub>2</sub> at 1° produced nearly as light a chip as those produced from tubers stored in air or 2.5% O<sub>2</sub> at 10°. 'Monona' and 'Norchip' accumulated more sucrose and less glucose and fructose than 'Kennebec' tubers during storage in air at 1° (Table 4). Storage in 2.5% O<sub>2</sub> at 1° reduced the sucrose accumulation of 'Monona' and 'Norchip' tubers, but it had essentially no effect on the 'Kennebec' sucrose level. Although storage in 2.5% O<sub>2</sub> reduced the accumulation of fructose and glucose in 'Kennebec' tubers stored at 1°, levels were still as high or higher than those of 'Monona' and 'Norchip' tubers stored in air at 1° (Table 4). Storage in N<sub>2</sub> at 1° kept the sucrose and reducing sugar levels of all 3 cultivars as low as 10° levels.

**Organic acids.** Malate and citrate were the only organic acids found in more than trace amounts. There were no consistently significant changes observed in citrate levels (data not presented). Changes in malate (Table 5) followed a pattern similar to that of sucrose and reducing sugars. The malate content of tubers stored in air at 1°C was more than double that of tubers stored at 10°. Storage in 2.5% O<sub>2</sub> decreased and storage in N<sub>2</sub> prevented this malate accumulation in potatoes stored at 1°.

## Discussion

Based on work with potato tissue slices, glycolysis, the tricarboxylic acid (TCA) cycle, and the pentose phosphate pathway are all considered to be potentially operative in potato tubers (3, 13). Norton (13) postulated that respiration in intact tubers is mediated by a largely malonate-resistant system, possibly a recycling pentose phosphate pathway, with a small amount of respiration via glycolysis and the TCA cycle. Shekhar and Iritani (17) suggested that the increased malate and citrate levels, which they observed in 'Russet Burbank' tubers stored at 5.5°C for 8 weeks, were related to increased respiratory rates, although respiratory data were not presented. This would seem to contradict reports that potato respiration is nearly minimal at 5.5° (3, 15, 16). Our results clearly show that malate content increased when tubers were stored in air at 1° (Table 5). Laties' (11) results indicated that increases in malate were associated with the increased TCA cycle activity of aged potato slices. The increases we observed in both CO<sub>2</sub> production and malate content of tubers stored in air at 1° suggest that TCA cycle activity is enhanced

during storage at 1°. The data for tubers stored in low O<sub>2</sub> atmospheres (2.5% O<sub>2</sub> and N<sub>2</sub>) are consistent with such an interpretation. Storage in 2.5% O<sub>2</sub> at 1° decreased CO<sub>2</sub> production and reduced the malate levels; storage in N<sub>2</sub> at 1° also reduced CO<sub>2</sub> production and kept malate levels as low as did 10° treatments (Fig. 1 and 2, Table 5).

Storage temperature dramatically affected the respiratory behavior of potatoes stored in N<sub>2</sub> (Table 1, Fig. 1 and 2). Barker and el Saifi (1) and Harkett (7) published similar results for potatoes stored in N<sub>2</sub> at 10° and 1°C, respectively. The differential respiratory behavior of potatoes stored in N<sub>2</sub> at 10° and 1° might appear to support the hypothesis that glycolysis is inhibited in potatoes stored at low temperatures (14). The soft rot which occurred in tubers stored in N<sub>2</sub> at 10° in both experiments may well have led to high respiration rates. This makes it impossible to conclude that the respiratory difference was due to a Pasteur effect at 10°. Barker and el Saifi (1) did not report any problems with soft rot in their experiments which involved storage in N<sub>2</sub> at 10° for up to 42 days. Perhaps the measurement of lactate production (2, 19) would be a better indicator of the Pasteur effect in potatoes, but it would be absolutely essential to have bacteria-free tubers.

Table 5. Effect of storage temperature and atmosphere on malate levels of 'Monona' and 'Norchip' tubers in the first experiment and 'Monona', 'Norchip', and 'Kennebec' tubers in the second experiment. Data are combined for cultivars.

Storage temp (°C)	Atmosphere	Malate (mm)	
		Expt. 1	Expt. 2
10	Air	2.5 <sup>z</sup>	1.7c <sup>y</sup>
1	Air	5.4	5.3a
10	2.5% O <sub>2</sub>	1.9	2.3c
1	2.5% O <sub>2</sub>	4.6	3.5b
10	N <sub>2</sub>	2.2	--- <sup>x</sup>
1	N <sub>2</sub>	2.4	1.5c

<sup>z</sup>Orthogonal comparisons for the interactions of temperature × (air vs. [2.5% O<sub>2</sub> + N<sub>2</sub>]) and temperature × (2.5% O<sub>2</sub> vs. N<sub>2</sub>) were significant at P = 0.01 and P = 0.001, respectively.

<sup>y</sup>Mean separation by Duncan's multiple range test, 5% level.

<sup>x</sup>All 10° N<sub>2</sub> treatments lost due to soft rot decay.

Harkett (7) reported that storage in low O<sub>2</sub> atmospheres (<3% O<sub>2</sub>) delayed, and storage in N<sub>2</sub> prevented, the sucrose and reducing sugar accumulation of 'Majestic' tubers stored at 1°C. Our results for 'Kennebec', 'Monona', and 'Norchip' tubers confirmed that storage in N<sub>2</sub> at 1° prevented the sucrose and reducing sugar accumulation. The success of the 2.5% O<sub>2</sub> atmosphere in blocking sucrose and reducing sugar accumulation depended on the sugar-forming characteristics of the cultivar. We have observed previously (5) that the ratio of sucrose to the reducing sugars was much greater in 'Norchip' stored at 1° than in 'Kennebec'. This relationship was verified in experiment 2. 'Monona' was intermediate in sucrose accumulation after chilling and like 'Norchip' had relatively low levels of reducing sugars at 1° in air (Table 4).

Storage in 2.5% O<sub>2</sub> substantially reduced the sucrose content of the 2 cultivars that accumulated high levels of sucrose in air at 1°C (Tables 3 and 4) but had no detectable effect on the sucrose content of 'Kennebec' (Table 4). There was also a cultivar difference in accumulation of the reducing sugars in 2.5% O<sub>2</sub> at 1°. 'Monona' and 'Norchip' had low levels of glucose and fructose; 'Kennebec' had higher levels. These cultivar differences in reducing sugars were reflected in chip color. Only 'Monona' and 'Norchip' produced acceptable chip color after storage in 2.5% O<sub>2</sub> at 1°.

Although all 3 cultivars gave light-colored chips when stored in N<sub>2</sub> at 1°C, it is obvious that the development of blackheart precludes this as a commercial practice. More research would be needed to know whether storage in 2.5% O<sub>2</sub> would have commercial potential. Aside from the question of commercial feasibility, further studies with reduced O<sub>2</sub> may be helpful in understanding the physiology of sugar accumulation at low temperatures.

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