Fatty Acids, Membrane Permeability, and Sugars of Stored Potato Tubers

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ABSTRACT

The relationships of potato (Solanum tuberosum L.) tuber membrane permeability and membrane lipid composition to sugar accumulation were examined. Tubers from four potato cultivars were stored for 40 weeks at 3°C and 9°C. Rates of tuber membrane electrolyte leakage, total fatty acid composition, free fatty acid composition, and sugar content were measured throughout the storage period. Storage of tubers at 3°C caused dramatic increases in total fatty acid unsaturation, membrane permeability, and sugar content compared to tubers stored at 9°C. Cultivars with higher levels of fatty acid unsaturation had lower rates of membrane electrolyte leakage and lower sugar contents. We propose that high initial levels or high induced levels of membrane lipid unsaturation mitigate increases in tuber membrane permeability during storage, thus positively influencing the processing quality of stored potato tubers.

Sucrose, glucose, and fructose are the major sugars which accumulate in potato (Solanum tuberosum L.) tubers. High levels of reducing sugars (glucose and fructose) lower the suitability of tubers for processing. Reducing sugars react with free amino groups during frying leading to the formation of a brown pigment, which can make chips and french fries (crisps and chips in the United Kingdom) unacceptable for consumers. Excess sugars in stored tubers commonly arise from two situations. Storage of tubers longer than 7 months can lead to 'senescent sweetening,' and storage below approximately 7°C can lead to 'cold-induced sweetening' (1). However, low temperature storage of potato tubers can also have the beneficial results of lowered respiration rates, slowed physiological aging, inhibition of sprouting, reduced evaporative water loss, and minimized microbial pathogenesis (1).

Sugars accumulate in tubers when there is an imbalance between starch degradation, starch synthesis, and respiration of carbohydrate. One potential source of metabolic imbalance is the cold-lability of PFK². It has been proposed that a reduction in PFK activity at low temperatures restricts glycolysis and leads to an increased hexose-phosphate content and a subsequent accumulation of sugars (7 and references therein). In addition to the cold, the activity of PFK and other enzymes of potato tuber carbohydrate metabolism can be influenced by the concentration and compartmentation of substrates, products, ions, cofactors, hormones, allosteric modifiers, and pH (13). If efficient compartmentation of these low mol wt molecules is necessary for the maintenance of a low sugar content, then the integrity of a tuber's cellular membranes becomes important. Several instances of reduced potato tuber membrane integrity during storage have been documented. Amyloplast membranes have been observed to physically deteriorate during extended long-term storage (8, 25). Reduced potato tuber membrane integrity measured as increased membrane electrolyte leakage has previously been implicated in the accumulation of sugars during low temperature storage (22, 29), extended term storage (8), and stem-end sweetening of Russet Burbank (22). In these instances, changes in either the physical status, or the chemical composition of the tuber membranes must account for the increased electrolyte leakage. Increased membrane lipid unsaturation is one chemical change that appears to confer resistance to increased electrolyte leakage in stored potato tubers (10).

Lipids represent approximately 0.1% of the fresh weight of a potato tuber (4, 5, 11). Greater than 94% of tuber lipids are in forms containing esterified fatty acids (4), of which greater than 70% are polyunsaturated fatty acids (18:2 and 18:3) (4, 5, 11, 19). Tuber lipid was found to consist of 47.4% phospholipid, 21.6% galactolipid, 6.4% esterified steryl glucoside, 1.3% sulpholipid, 2.4% cerebrosides, and 15.4% triglyceride (4). These major lipids and a portion of the triglycerides are associated with the tuber membranes (5, 19). While lipid bodies can occasionally be found within the cytoplasm (19), it is unlikely that tubers contain appreciable amounts of lipid reserves (5). Thus, the total fatty acid composition of potato tubers should primarily reflect the composition of cell membranes (5).

Several chemical or physical changes can occur to a membrane’s component fatty acids which can lead to increased membrane permeability: (a) peroxidation of unsaturated fatty acids.

1 From a dissertation submitted to the graduate school of the University of Minnesota by J. P. S. in partial fulfillment of the requirements for the Ph.D. degree. The research was supported by the Minnesota Agricultural Experiment Station and by a grant from the Frito-Lay Co., Inc. This is Minnesota Agricultural Experiment Station Paper No. 17,963. Scientific Journal Series.

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3 Abbreviations: PFK, phosphofructokinase; FFA, free fatty acid; CIPC, isopropyl N-(3-chloro-phenyl) carbamate; 2-NPH, 2-nitrophenylhydrazine; 1-EDC-HCl, 1-ethyl-3-[3(dimethylamino-propyl)carbodiimide; gfw, gram of fresh weight; 16:0, palmitic acid; 18:0, stearic acid; 18:1, oleic acid; 18:2, linoleic acid; 18:3, linolenic acid.
acyl-lipids (12, 15, 18, 23, 27, 28), (b) deesterification and accumulation of FFA in the blayer (6, 9, 15, 20, 21), (c) loss of diacylglycerol-lipids (15, 20, 21, 23, 27), or (d) transition of membranes and their component acyl-lipids from a normal flexible liquid-crystalline structure to a solid gel structure at a critical low temperature (15, 18, 20, 21, 23, 27, 28, 30). Our objectives were to determine if tuber membrane fatty acyl-lipid composition could account for alterations in membrane permeability, and if membrane permeability could influence potato tuber sugar content and subsequent processing quality.

**MATERIALS AND METHODS**

**Growth and Storage of Potatoes**

The potato (*Solanum tuberosum* L.) cultivars studied were Red Pontiac and Russet Norgold (high-sugar cultivars), and Norchip and Monona (low-sugar cultivars). The tubers were mechanically harvested, placed into wooden crates and held in darkness for 2 weeks at ambient room temperature prior to storage at either 3 or 9°C. The tubers stored at 9°C were treated with a gaseous application of the sprout inhibitor CIPC during the sixth week of storage. Tubers stored at 3°C were not treated with CIPC.

**Chemicals**

Glucose, fructose, sucrose, cellobiose, pyridine, 2-NPH and 1-EDC-HCl were obtained from Sigma Chemical Co. Hexadecanoic acid was obtained from Aldrich Chemical Co., Inc. An equimolar fatty acid methyl ester mixture was obtained from Supelco, Inc. (Bellefonte, PA). Isopropanol was of technical grade (Ashland Oil Co., Inc., Shakopee, MN). All other solvents and chemicals were of reagent grade.

**Potato Chip Color Assay**

Two 1.5 mm slices were removed from each of eight tubers, rinsed with water, and placed into 190°C cooking oil for 100 s. The color of the resulting chips was determined by measuring the reflection of 640 nm light from crushed chips in a reflection spectrophotometer (model M-400-A Agtron, Magnuson Engineers, Inc., San Jose, CA). Chip color was expressed as ‘agtron units,’ where black = 0 agtron units and white = 100 agtron units.

**Electrolyte Leakage Assay**

Electrolyte leakage measurements were based upon the method of Workman et al. (29). Cores were removed from each of eight tubers and sliced to yield three 3 mm·9 mm discs, representing the central pith, midparenchyma, and cortex of the tuber tissue. The 24 discs were rinsed, placed into 40 mL water, and gently tumbled at ambient room temperature. Conductance of the water was measured after 15 min (C1), 2 h (C2), and 2 h after a freeze-thaw treatment (Ctotal). The rate of electrolyte leakage was expressed as: %/h = 100·(C2 - C1)/(1.75·Ctotal).

**Sugar Assay**

Sugars were extracted from tuber tissue (100 g) according to the method of Sowokinos et al. (25), and a 10 mL aliquot of extract was lyophilized. The lyophilized samples were mixed for 30 min at 60°C with 10 mL of acetonitrile:water (73:27, v/v) which contained cellobiose (1.4 g/L) as an internal standard. Chromatography was performed at room temperature through a 4.6 mm·250 mm column which contained 5 μm particle Ultrahex amino stationary phase (Phenomenex, Torrance, CA). The mobile phase was acetonitrile:water (73:27, v/v) delivered at a rate of 1 mL/min. The refractive index of the column eluent was monitored and recorded as peak areas. Column loads contained 140 μg cellobiose per 100 μL injection.

**Total Fatty Acid Assay**

Total lipid extraction from tubers (100 g) was accomplished according to method C of Fishwick and Wright (3). Heptadecanoic acid (18.7 mg) was included in the extraction as an internal standard. Saponification, derivitization, and chromatography were performed according to the methods of Miwa et al. (16). Chromatography utilized a 4.6 mm·250 mm column which contained 5 μm particle IB-SIL C-8 stationary phase (Phenomenex) heated to 40°C. The mobile phase was 82% methanol in water (v/v, acidified to pH 4.5 with HCl) delivered at a rate of 1.25 mL/min. Column loads contained approximately 2 μg heptadecanoic acid per 200 μL injection.

**Free Fatty Acid Assay**

The extraction of free fatty acids from tubers (100 g) was the same as for total fatty acids with the exception that the heptane-isopropanol-water solvent system of Dole and Meinertz (2) was substituted for the chloroform-methanol-water system of Fishwick and Wright (3). Heptadecanoic acid (5.6 mg) was included in the extraction as an internal standard. The FFAs contained in the heptane phase were derivitized and chromatographed according to the methods of Miwa et al. (16). Column loads contained approximately 20 μg of heptadecanoic acid per 200 μL injection.

**Experimental Design and Statistical Analysis**

For all assays an experimental unit consisted of tissue pooled from each of eight tubers which had been peeled and diced. All measurements were replicated three times; 24 tubers contributed to each mean. Linear regressions, analyses of variance, subsequent calculations of least significant differences and multiple comparisons of means (Student-Newman-Keuls Test) were performed with the data. The data were organized in a completely randomized design with a factorial set of treatments where cultivar, storage temperature, and sampling time were the main effects. Data from the preharvest and prestorage treatments were not included in the statistical analyses. The significance level (P value) of a correlation is given when the slope of a pooled linear regression line of all four cultivars is cited to be significantly different from zero.
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RESULTS

The potato tubers remained turgid and without sprouts throughout the entire 40 weeks of storage. Tubers had higher rates of electrolyte leakage during 3°C storage than 9°C (Table I). Electrolyte leakage also increased during the last 18 weeks of storage at 9°C (P < 0.001) (Fig. 1A). Cultivars differed in their rates of electrolyte leakage with Red Pontiac > Russet Norgold > Norchip > Monona (Table I). Tubers stored at 3°C had higher sucrose and reducing sugar contents compared with tubers stored at 9°C (Table I). Potato chips were much darker from tubers out of 3°C storage than 9°C storage (Table I). The four cultivars differed greatly in their rates of electrolyte leakage, sugar content, and chip color (Table I). Rates of tuber electrolyte leakage and sugar contents fluctuated with the length of time in storage at 3°C but were comparatively stable during 9°C storage (Fig. 1, A–C). Chip color was also fairly stable throughout storage at both temperatures, although chips out of 3°C storage were becoming brighter during the last 18 weeks of storage (P > 0.001) (Fig. 1D).

When the data from all four cultivars were combined, reducing sugar content was negatively correlated with chip color (r = −0.94, P < 0.001) (Fig. 2A). Potato chip color was negatively correlated with the rates of electrolyte leakage (r = −0.88, P < 0.001) (Fig. 2B) and electrolyte leakage was positively correlated with reducing sugar content (r = 0.83, P < 0.001) (Fig. 2C).

For clarity, composite representations of the fatty acid data are shown (Fig. 3, A–C). All individual cultivars demonstrated patterns of change similar to the composite representations. Total fatty acid content (calculated as the sum of total 16:0, 18:0, 18:1, 18:2, and 18:3) declined during the 10 months of storage at 3°C (P < 0.01) and at 9°C (P < 0.001) (Fig. 3A). During the 3°C storage treatment, total fatty acid content was lower compared to the 9°C temperature treatment in Red Pontiac and Russet Norgold, but not Norchip or Monona (Table II).

The ratio of total linolenic acid (18:3) to linoleic acid (18:2) increased during storage at both temperatures (P < 0.001 and P < 0.001) (Fig. 3B). Depending upon the cultivar, the 18:3/18:2 ratio was 32 to 41% higher during storage at 3°C compared to 9°C (Table III). At the same time the total molar sum of these two polyunsaturated fatty acids remained constant between cultivars and between temperature treatments at 70.8 to 71.7% (Table III). Palmitic, stearic, and oleic acids accounted for the remaining 21.0%, 6.0%, and 1.7% of total fatty acids respectively (data not shown). Cultivar dependent differences existed in the degree of unsaturation (18:3/18:2 ratio) with Monona > Norchip > Russet Norgold > Red.

Figure 1. Changes during storage in (A) rates of electrolyte leakage, (B) sucrose content, (C) glucose and fructose content, and (D) chip color of potato tubers. Chips with color values greater than 55 are acceptable for commercial use. The symbols are from Red Pontiac (□ or ■), Russet Norgold (○ or ◆), Norchip (Δ or ▲), and Monona (○ or ◆). Filled symbols are values from the 3°C storage treatment. Open symbols are values from the preharvest, prestorage, or 9°C storage treatments. Each symbol is a mean of three measurements. The LSD0.05 applies to means from the storage treatments. To accommodate the preharvest and prestorage measurements, the x-axes begin at −5 weeks of storage.
Table I. Electrolyte Leakage, Sugar Content, and Chip Color of Potato Tubers Stored at 9°C or 3°C

Values listed are composite means for the entire 40 week storage period. Each composite mean represents 21 measurements (three replications of each cultivar at each of the seven sampling dates during storage). Values with the same letter do not differ significantly (P < 0.05). The second column of letters indicates statistical significance when the data from the two temperature treatments were combined.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Storage Temperature</th>
<th>Electrolyte Leakage</th>
<th>Sucrose</th>
<th>Glucose + Fructose</th>
<th>Chip Color</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>°C</td>
<td>%/h</td>
<td>mg/gfw</td>
<td>units</td>
<td></td>
</tr>
<tr>
<td>Red Pontiac</td>
<td>9</td>
<td>1.30 d</td>
<td>1.65 d</td>
<td>6.04 e</td>
<td>31.4 c</td>
</tr>
<tr>
<td>Red Pontiac</td>
<td>3</td>
<td>4.58 a</td>
<td>6.79 b</td>
<td>27.42 a</td>
<td>10.4 g</td>
</tr>
<tr>
<td>Russet Norgold</td>
<td>9</td>
<td>1.08 de</td>
<td>0.93 e</td>
<td>6.00 e</td>
<td>29.9 c</td>
</tr>
<tr>
<td>Russet Norgold</td>
<td>3</td>
<td>2.64 b</td>
<td>5.75 c</td>
<td>24.38 b</td>
<td>12.4 f</td>
</tr>
<tr>
<td>Norchip</td>
<td>9</td>
<td>0.96 e</td>
<td>1.14 de</td>
<td>0.86 f</td>
<td>59.4 b</td>
</tr>
<tr>
<td>Norchip</td>
<td>3</td>
<td>2.50 b</td>
<td>11.55 a</td>
<td>13.69 c</td>
<td>19.6 e</td>
</tr>
<tr>
<td>Monona</td>
<td>9</td>
<td>0.89 e</td>
<td>0.93 e</td>
<td>1.31 f</td>
<td>61.4 a</td>
</tr>
<tr>
<td>Monona</td>
<td>3</td>
<td>1.71 c</td>
<td>5.58 c</td>
<td>12.35 d</td>
<td>22.3 d</td>
</tr>
</tbody>
</table>

Poncia (Table III). When a correlation was made across all four cultivars stored at 3°C, the rate of electrolyte leakage was found to be negatively correlated with the degree of fatty acid unsaturation (r = −0.47, P < 0.001) (Fig. 2D). This overall correlation was not significant when the tubers were stored at 9°C. On an individual cultivar basis, the rate of electrolyte leakage was found to be negatively correlated with the degree of fatty acid unsaturation in the case of Red Pontiac stored at 3°C (r = −0.70, P < 0.001) and positively correlated in the case of Monona at 3°C (r = 0.76, P < 0.001) (Fig. 2E). Correlations were not significant for Russet Norgold or Norchip.

Tuber FFA levels were calculated as the sum of free palmitic (16:0), oleic (18:1), linoleic (18:2), and linolenic (18:3) acids, which accounted for 30.1, 9.0, 40.3, and 20.5% of the FFAs, respectively (data not shown). Free steric acid was detected but not reliably quantitated. FFA levels were higher during 3°C storage compared to 9°C storage for all cultivars except Red Pontiac (Table II). Cultivars differed in FFA content with Monona < Red Pontiac < Norchip < Russet Norgold (Table II). When expressed as a percentage of total fatty acids, there was a decrease in the percentage of FFAs in tubers stored at 9°C (P < 0.01) (Fig. 3C) but if the data from week 34 were considered outliers and omitted, the decrease during 9°C storage was not significant. However, over the 40 weeks of storage at 3°C, there was a highly significant decline in the FFA content of tubers (p < 0.001) (Fig. 3C).

**DISCUSSION**

Potato chips with agron values greater than 55 are suitable for commercial use. It is generally accepted that reducing sugar content is responsible for the determination of potato chip color, so it is no surprise that in our experiment the two parameters were found to be negatively correlated (r = −0.94) (Fig. 2A). However, we also found that rates of membrane electrolyte leakage were positively correlated with reducing sugar content (r = 0.83) (Fig. 2C), and negatively correlated with chip color (r = −0.88) (Fig. 2B). Rates of electrolyte leakage from plant cells can be used as an index of plasma membrane permeability, and probably permeability of the tonoplast as well (23). Thus, the correlations mentioned above would seem to indicate an involvement of tuber membrane permeability in mechanisms that lead to sugar accumulation and a subsequent decline in chip color.

Many plant tissues including potato tubers have been shown to increase the degree of unsaturation of their membrane fatty acids in response to low temperatures (14, 15, 26, 27, 30). Increased membrane lipid unsaturation during low temperature exposure has been interpreted as a beneficial acclimation response. Recently, Steponkus et al. (26) have moved beyond correlative findings and have definitively shown that increased lipid unsaturation can impart enhanced cryobehavior to rye plasma membranes. Increased unsaturation of membrane lipids with low temperatures, or conversely decreased fatty acid unsaturation with high temperatures appears to be a mechanism by which biological membranes regulate membrane viscosity (24). Therefore, membranes of potato tubers from the cultivars Monona (Table II) or the popular British chipping cultivar Record (5), which contain the highest constitutive or induced levels of fatty acid unsaturation, may best retain their fluidity when exposed to low storage temperatures.

It is important to note that when cultivars were ranked by their degree of fatty acid unsaturation (Table III), this was the opposite of their rank by rate of membrane electrolyte leakage (Table I). When the data were combined across all four cultivars, total fatty acid unsaturation was found to be negatively correlated with electrolyte leakage (r = −0.47) (Fig. 2D). Knowles and Knowles (10) obtained a similar result. They found that when tubers of the cultivar Russet Burbank were stored for 32 months at 4°C the double bond index of...
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Figure 3. Changes during storage in (A) total fatty acid content (calculated as the sum of total 16:0, 18:0, 18:1, 18:2, and 18:3); (B) total linolenic acid versus total linoleic acid ratio; (C) free fatty acid content (expressed the molar sum of free 16:0, 18:1, 18:2, and 18:3 versus total molar fatty acid content). In (A–C) each symbol is a composite mean of 12 measurements (three replications of each of the four cultivars), from either the preharvest (●), prestorage (▲), 3°C storage (●), or 9°C storage (○) treatments. Note that in (A–C) neither the x-axes or y-axes begin at 0.

Figure 2. Correlations of (A) potato chip color versus glucose and fructose content, \( y = 53.3 - 0.94x \); (B) potato chip color versus rates of electrolyte leakage, \( y = 49.0 - 0.08x \); (C) glucose and fructose content versus rates of electrolyte leakage, \( y = 6.50 - 1.54x \); (D) electrolyte leakage versus the 18:3/18:2 ratio at 3°C (all cultivars), \( y = 1.28 - 10.9 \log x \); and (E) electrolyte leakage from Pontiac (○) and Monona (●) versus the 18:3/18:2 ratio at 3°C, \( y_{\text{Pontiac}} = 2.14 \cdot x^{1.78} \), and \( y_{\text{Monona}} = 4.62 \cdot x - 2.11 \). In (A–D) the symbols do not distinguish between cultivars or temperature treatments. In (A–E) each symbol is a single measurement.
tuber fatty acids was negatively correlated \((r = -0.97)\) with electrolyte leakage. The stronger negative correlation attained by Knowles and Knowles can likely be attributed to their use of only a single cultivar and to a superior electrolyte leakage assay.

The extent of the decline in total fatty acid content over 10 months of storage was approximately 10% of the total fatty acids (Fig. 3A) and cold storage reduced total fatty acid content in two of the four cultivars only 3 to 6% (Table II). It is assumed that these changes in total fatty acid content represent changes in the membrane acyl lipid content of the tubers. It is possible, although unlikely, that such slight changes in fatty acid content could fully account for the increased membrane permeability during the low temperature storage or extended term storage.

FFA levels in plants have been shown to increase several-fold with cold stress (6), dehydration stress (20, 21), and artificial aging (28). In these instances the high levels of FFAs were considered detrimental to membrane function. It has also been demonstrated through in vitro systems that saturated FFAs (9), or mixtures of saturated and unsaturated FFAs (21) have the ability to reduce membrane fluidity. The accumulations of FFAs in plants under the above stress conditions (6, 20, 21, 28) were associated with a simultaneous loss of membrane diacylglycerol-lipids. It is unknown if the FFAs detected in our experiment were formerly membrane acyl lipids, and if so, whether the FFAs were released by the tuber's lipid acyl hydrolase activity (12, 17) or by free radical des-esterification (15, 20), or even if the detected FFAs were located within membrane bilayers prior to extraction.

To test the ability of individual FFAs to shift the phase transition temperatures of dipalmitoyl lecithin bilayers, Jain and Wu (9) demonstrated that a FFA (palmitic acid) content of 4.9% (mol/mol) was necessary to raise the liposome phase transition temperature by 1°C. The unsaturated FFAs (18:1, 18:2, and 18:3) were effective in similar concentrations, but instead the unsaturated FFAs lowered phase transition temperatures. In a similar experiment microsomes isolated from nonstressed imbibed soybean axes contained a FFA content of 3.4% (mol/mol phospholipid). To mimic the effects of a

### Table II. Total Fatty Acid Content and Free Fatty Acid Content of Potato Tubers Stored at 9°C and 3°C

The statistical description of each value is the same as in Table I.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Storage Temperature</th>
<th>Total Fatty Acid Content</th>
<th>Free Fatty Acid Content</th>
<th>mol FFA/gfw</th>
<th>mol Total FA/gfw</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>°C</td>
<td>µg/gfw</td>
<td></td>
<td>%</td>
<td></td>
</tr>
<tr>
<td>Red Pontiac</td>
<td>9</td>
<td>681 b</td>
<td>2.55 b</td>
<td>0.375 b</td>
<td></td>
</tr>
<tr>
<td>Red Pontiac</td>
<td>3</td>
<td>669 c</td>
<td>2.63 b</td>
<td>0.401 b</td>
<td></td>
</tr>
<tr>
<td>Russet Norgold</td>
<td>9</td>
<td>736 a</td>
<td>2.75 b</td>
<td>0.381 b</td>
<td></td>
</tr>
<tr>
<td>Russet Norgold</td>
<td>3</td>
<td>693 b</td>
<td>3.05 a</td>
<td>0.447 a</td>
<td></td>
</tr>
<tr>
<td>Norchip</td>
<td>9</td>
<td>680 bc</td>
<td>2.57 b</td>
<td>0.381 b</td>
<td></td>
</tr>
<tr>
<td>Norchip</td>
<td>3</td>
<td>674 bc</td>
<td>3.11 a</td>
<td>0.471 a</td>
<td></td>
</tr>
<tr>
<td>Monona</td>
<td>9</td>
<td>647 d</td>
<td>1.86 d</td>
<td>0.295 c</td>
<td></td>
</tr>
<tr>
<td>Monona</td>
<td>3</td>
<td>636 d</td>
<td>2.30 c</td>
<td>0.369 b</td>
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</table>

### Table III. Linoleic (18:2) and Linolenic Acid (18:3) Composition of Potato Tubers Stored at 9°C and 3°C

The statistical description of each value is the same as in Table I.

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>Storage Temperature</th>
<th>Partial FA Profile</th>
<th>mol % 18:3</th>
<th>mol % 18:3 + mol % 18:2</th>
<th>mol % of total FA</th>
<th>mol % of total FA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>°C</td>
<td></td>
<td>18:2</td>
<td>18:3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Red Pontiac</td>
<td>9</td>
<td>48.9 a</td>
<td>22.9 f</td>
<td>0.470 f</td>
<td>71.8 a</td>
<td>70.8 a</td>
</tr>
<tr>
<td>Red Pontiac</td>
<td>3</td>
<td>42.7 d</td>
<td>28.2 c</td>
<td>0.663 c</td>
<td>&gt;d</td>
<td>70.8 a</td>
</tr>
<tr>
<td>Russet Norgold</td>
<td>9</td>
<td>47.0 b</td>
<td>24.2 e</td>
<td>0.517 e</td>
<td>&gt;c</td>
<td>71.2 a</td>
</tr>
<tr>
<td>Russet Norgold</td>
<td>3</td>
<td>42.6 d</td>
<td>29.1 b</td>
<td>0.685 c</td>
<td>&gt;c</td>
<td>71.7 a</td>
</tr>
<tr>
<td>Norchip</td>
<td>9</td>
<td>46.3 b</td>
<td>24.8 e</td>
<td>0.538 e</td>
<td>&gt;b</td>
<td>71.1 a</td>
</tr>
<tr>
<td>Norchip</td>
<td>3</td>
<td>41.7 e</td>
<td>29.7 b</td>
<td>0.714 b</td>
<td>&gt;b</td>
<td>71.4 a</td>
</tr>
<tr>
<td>Monona</td>
<td>9</td>
<td>44.2 c</td>
<td>27.0 d</td>
<td>0.613 d</td>
<td>&gt;a</td>
<td>71.1 a</td>
</tr>
<tr>
<td>Monona</td>
<td>3</td>
<td>39.1 f</td>
<td>32.2 a</td>
<td>0.828 a</td>
<td>&gt;a</td>
<td>71.3 a</td>
</tr>
</tbody>
</table>
dehydration stress FFAs were added to the microsomes to raise the FFA content to 37.4%; this treatment elevated the phase transition temperature of the microsomes by 31°C (21).

A number of other stresses have been shown to increase the FFA (mol/mol phospholipid) content of several plants (reviewed in McKersie et al. [15]); soybean seeds during natural aging, 3 to 64%; wheat crowns exposed to freezing stress, 23 to 260%; and cucumber chloroplasts under chilling stress, 5.3 to 46% (mol/mol galactolipid) (6). Combining the results of all four potato cultivars during the entire storage period at 9°C, tubers contained 0.24% FFA (mol/mol total fatty acid). This ratio increased to 0.30% during the 3°C storage. To roughly approximate FFAs per mole of diacylglycerol-lipid these figures can be doubled to 0.48 and 0.60%, respectively.

Even if all of the detected tuber FFAs were located within membrane bilayers, these concentrations of FFA are very low compared to the FFA levels found in the other plant tissues listed above or when compared to the concentrations necessary to evoke a 1°C shift in phase transition temperatures of artificial liposomes (9). Thus it is unlikely that the higher levels of FFAs contained in tubers during 3°C storage compared to 9°C had any appreciable effect upon tuber membrane fluidity.

In conclusion we propose that: (a) High or increased rates of tuber membrane permeability negatively influenced the sugar status and processing quality of stored tubers. (b) Induced or initial high levels of membrane lipid unsaturation mitigated increases in tuber membrane permeability during storage. (c) The alterations in the levels of FFA and total fatty acid encountered in this experiment had little bearing upon tuber membrane permeability. If these conclusions are valid, then genetic alterations which increase the proportion of linolenic acid in membrane lipids may enhance the processing characteristics of the tuber out of low temperature storage.

LITERATURE CITED