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Comparison of Fatty Acid and Polar Lipid Contents of Tubers from Two Potato Species, *Solanum tuberosum* and *Solanum phureja*

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Total and individual fatty acid contents were determined in raw tubers of four genotypes from each of the two species *Solanum phureja* and *S. tuberosum*. The four *S. phureja* genotypes contained statistically significantly higher concentrations of total fatty acids, with their average value being 37% greater than that for the mean of the four *S. tuberosum* cultivars. In both species, a total of 17 fatty acids were detected in quantifiable amounts, and in all genotypes the predominant fatty acid was linoleic followed by α-linolenic and palmitic acids. Unusually, 15-methyl hexadecanoate was present as a minor acid in both species. Although a number of statistically significant differences in the fatty acid percentage compositions were found between and within the two species, these were generally small. Averaged over all species and genotypes, tuber storage resulted in an initial small but statistically significant increase in total fatty acid content, but prolonged storage resulted in a fall to the initial values detected close to harvest. The same trend was evident for *S. phureja* alone (for mean values of all genotypes), but for *S. tuberosum* the total fatty acid content remained constant over the whole storage period. For both species, the contents (both as absolute levels and as percent compositions) of linoleic acid decreased and α-linolenic acid increased in tubers over the whole storage period, and possible mechanisms are discussed. Also, the absolute levels of these two acids were greater in *S. phureja* than in *S. tuberosum*, and this is discussed in relation to the development of flavor-related compounds during cooking. The polar lipids of one representative of *S. tuberosum* and of *S. phureja* were qualitatively similar. There were only minor differences in the polar lipid percentage compositions and in the corresponding fatty acid compositions of the individual polar lipids between the two species, although the absolute levels of the total, and of some individual, polar lipids were higher in *S. phureja*.

KEYWORDS: Potato; flavor; fatty acids; lipids; storage; *Solanum tuberosum*; *Solanum phureja*

INTRODUCTION

The majority of established culinary potato cultivars belong to the conventional tetraploid species *Solanum tuberosum*. However, there is currently considerable interest in the diploid species *S. phureja*, developed from the Andean cultivated potato (*1*, *2*). Tubers from *S. phureja* clones have been selected that are resistant to soft rot, a property that is rare in *S. tuberosum* (*1*). *S. phureja* also has a yellower flesh (due to higher levels of carotenoids) than *S. tuberosum* and in sensory analysis has distinctive mouth-feel characteristics (high in smooth and low in grainy and floury traits) and a higher intensity of flavor attributes (creamy, sour, earthy) than *S. tuberosum* (*2*). The content (1−6 mg 100 g^{-1} of fresh weight) of potentially toxic glycoalkaloids in tubers of *S. phureja* genotypes was below both the recommended maximum concentration for human consumption and the level (15 mg 100 g^{-1} of fresh weight) at which a bitter flavor may result (*3*). *S. phureja* populations are therefore promising as a source of specialist cultivars grown for flavor and as a gene pool that could be introgressed into the higher yielding *S. tuberosum*.

Raw potato contains low levels of flavor volatiles, and the process of cooking (boiled, baked, or fried) influences flavor generation, partly as a result of temperature (*4*, *5*). Precursors of flavor volatiles include reducing sugars and amino acids that are notably involved in the production of pyrazines (responsible for a typical earthy "potato-like" flavor) formed by Maillard (nonenzymic browning) reactions. Amino acids produce branched-chain carbonyl and alcohol volatiles by Strecker degradation, whereas straight-chain volatiles, including aldehydes, ketones and alcohols, and alkyl furans, are derived by oxidation

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(autoxidation or enzymic) of unsaturated fatty acids (mainly linoleic and α-linolenic acids), which are present in the potato mainly as components of polar lipids. The importance of fatty acid oxidation products in contributing to the volatile profile and flavor of boiled potatoes is well documented (*4*−*9*). Fatty acid-derived volatiles have been considered to generally contribute to unpleasant notes in potato; for example, hexanal and 2-pentylfuran contribute "green" flavors, whereas 2,4-decadienal has a "fatty" character (*9*). In contrast, there is evidence that 4*Z*-heptenal imparts a "boiled potato-like aroma" to boiled potatoes, and addition of this compound to mashed potatoes either enhanced the earthy, potato-like flavor (low levels) or imparted a stale flavor (higher levels) (*6*).

In the present study, as part of our efforts to understand the differences in flavor between *S. phureja* and *S. tuberosum*, the fatty acid and lipid compositions of representative cultivars and genotypes of the two species were compared.

MATERIALS AND METHODS

Plant Material. The genotypes utilized in this study were selected on the basis of their taste characteristics as determined by professional taste panels. The four *S. tuberosum* cultivars (Ailsa, Cara, Maris Piper, and Pentland Dell) represented the more "bland" cultivars, whereas the four *S. phureja* genotypes (DB 257/28, DB 333/16, DB 337/37, and DB 358/23) were selected for their more "distinct" flavor characteristics (*2*).

All genotypes were harvested from field plots grown using normal agronomic practices at a trial site located at Mylnefield, Dundee, U.K., in 2000. The tubers were harvested 2 weeks following foliage burndown, stored at ambient temperature (.∼8−12 °C) for 4 weeks to allow for skin set, and then transferred to a 4 °C store.

At 4, 10, and 21 weeks postharvest, two replicate samples of the eight genotypes were removed from the cold store. Each replicate consisted of six average-sized tubers, which were chopped into eighths; two opposite eighths from each tuber were quickly diced, immersed in liquid nitrogen, and bulked by replicate. The sample was then freeze-dried, ground in a laboratory mill fitted with a 1 mm screen, and stored in the dark at −20 °C until required for analysis.

Chemicals. Most standards and reagents were purchased from Sigma-Aldrich Co. Ltd. (Poole, U.K.). Solvents were of HPLC or Distol grade and were supplied by Fisher Scientific U.K. (Loughborough, U.K.).

Chemical Analysis. Dry matter content was determined on the basis of weight difference before and after freeze-drying. The results were expressed in terms of grams of freeze-dried matter per 100 g of fresh weight (g of FDM 100 g^{-1} of FWt).

Preparation of Fatty Acid Methyl Esters (FAME). FAME were prepared by direct sulfuric acid catalyzed transesterification of freeze-dried potato powder. Toluene (0.75 mL), nonadecanoic acid methyl ester [internal standard (21.3 mg in 100 mL of methanol; 0.25 mL], and 1% (v/v) methanolic sulfuric acid (2 mL) were added to the freeze-dried potato (50 mg) in a stoppered tube. The tube was left overnight at 50 °C on a heating block and, after cooling, 5% (w/v) sodium chloride (5 mL) and isohexane (3 mL) were added; the mixture was shaken and centrifuged. The upper organic layer was removed, and the aqueous layer was re-extracted with isohexane (3 mL). The combined organic layers were washed with 2% (w/v) potassium hydrogen carbonate (3 mL) and then passed through a short (3 cm) column of anhydrous sodium sulfate prepared in a Pasteur pipet. The column was washed with isohexane, and the combined eluents, containing the FAME, were taken to dryness under nitrogen at 30 °C on a heating block. The FAME were dissolved in isohexane containing butylated hydroxytoluene (50 ppm) and kept at −20 °C until they were analyzed.

Preparation of 4,4-Dimethyloxazoline (DMOX) Derivatives. The FAME were hydrolyzed with 0.1 M potassium hydroxide in 90% aqueous ethanol (0.25 mL mg^{-1} of sample) at 50 °C for 3 h. After acidification with acetic acid and addition of water (2 mL), the free fatty acids were extracted twice with diethyl ether/isohexane (1:1, by vol; 6 mL and then 3 mL). The combined organic layers were passed through a short (3 cm) column of anhydrous sodium sulfate prepared in a Pasteur pipet and were taken to dryness under nitrogen at 30 °C on a heating block.

The free fatty acids were converted to DMOX derivatives by heating with 2-amino-2-methyl-1-propanol (0.25 mL) at 190 °C for 16 h. On cooling, water (5 mL) was added and the DMOX derivatives were extracted with diethyl ether/isohexane (1:1, by vol; 5 mL). The aqueous layer was re-extracted with fresh solvent (2 mL), and the combined solvent extracts were washed with water (3 mL) and dried over anhydrous sodium sulfate. Finally, the solvent extract was passed through a short (3 cm) column of anhydrous sodium sulfate prepared in a Pasteur pipet. The column was washed with isohexane, and the combined eluents, containing the DMOX derivatives, were taken to dryness under nitrogen at 30 °C on a heating block. The DMOX derivatives were dissolved in isohexane containing butylated hydroxytoluene (50 ppm) and kept at −20 °C until they were analyzed.

Gas Chromatography (GC) of FAME. GC of FAME was performed using a Hewlett-Packard model 5890 series II gas chromatograph equipped with a split/splitless injector, an autosampler, and a flame ionization detector. A capillary column of fused silica coated with CP-Wax 52CB (0.25 mm i.d. × 25 m in length, 0.2 μm film thickness; Chrompack U.K. Ltd., London. U.K.) was used, and hydrogen was the carrier gas at an initial flow rate of 1 mL/min. After the temperature had been held at 170 °C for 3 min, the column was temperature-programmed at 4 °C min^{-1} to 220 °C and then was held at this point for a further 15 min. The detector was set at 300 °C and the injector at 230 °C, and a split ratio of 50:1 was used. An HP 3365 Chemstation (Hewlett-Packard Ltd., Stockport, U.K.) was used for data acquisition.

Gas Chromatography−Mass Spectrometry (GC-MS) of FAME and DMOX Derivatives. FAME and DMOX derivatives were analyzed by GC-MS on a Hewlett-Packard 5890 series II Plus gas chromatograph, fitted with an on-column injector and a Supelcowax 10 (0.25 mm × 30 m, 0.25 μm) capillary column, connected to a Hewlett-Packard 5989B MS Engine quadrupole mass spectrometer. The column temperature was held at 80 °C for 3 min, temperature-programmed to 170 °C at 20 °C min^{-1} and then to 240 °C at 2 °C min^{-1} followed by 280 °C at 5 °C min^{-1}, and was finally held at 280 °C for 15 min. Helium was the carrier gas, at a flow rate of 1.4 mL min^{-1}, and pressure-programming was used in constant-flow mode. The mass spectrometer was operated in electron impact mode at an ionization energy of 70 eV.

Extraction of Total Lipids. Each of four potato tubers was cut into eight pieces, and two opposing eighths of each were pooled, chopped, and mixed; a proportion (∼30 g) was immediately immersed in 2-propanol (80 mL) at 80 °C. After the addition of internal standards of diheptadecanoyl phosphatidylcholine and trinonadecanoin (0.6 mg of each dissolved in chloroform/propan-2-ol, 1:1, v/v), the mixture was refluxed for 15 min, allowed to cool, and homogenized for 5 min with an Ultra-Turrax blender. Chloroform (80 mL) was added, homogenization was continued for a further 3 min, and the mixture was filtered through Whatman no. 1 filter paper (prewashed with 30 mL of chloroform/2-propanol, 1:1 v/v, 30 mL). The residue was re-extracted with chloroform/methanol (2:1, v/v, 100 mL) by homogenization for 5 min, filtered, and washed with more chloroform/methanol (2:1, v/v, 50 mL). The solvents were removed from the combined extracts at 40 °C on a rotary evaporator. The lipid material was dissolved in chloroform/methanol (2:1, v/v) and centrifuged, and the supernatant was passed through a PTFE filter (Whatman Puradisc 25 TF, 0.2 μm). The extract was subjected to a Folch wash to remove nonlipid contaminants. Chloroform/methanol/0.88% (w/v) aqueous potassium chloride was added to the mixture so that the final proportions were 8:4:3 (by vol). The mixture was shaken, the upper aqueous layer discarded, and the lower layer washed with methanol/0.88% aqueous potassium chloride (1:1, v/v, one-fourth volume of lower layer) and taken to dryness under nitrogen at 40 °C on a heating block. All solvents used for extraction contained butylated hydroxytoluene (50 ppm). The lipid was kept at −20 °C in isohexane containing butylated hydroxytoluene (50 ppm) until analysis.

Analysis of Polar Lipids. Polar lipid classes in total lipid extracts (dissolved in chloroform/methanol, 2:1, v/v) were separated prepara-

Table 1. Total Fatty Acid Content of Stored Tubers from Four Genotypes from Each of the Two Potato Species, *S. tuberosum* and *S. phureja*

		μg g^{-1} of fresh wt after postharvest storage period of				μg g^{-1} of freeze-dried matter after postharvest storage period of			
species	genotype	4 weeks	10 weeks	21 weeks	mean	4 weeks	10 weeks	21 weeks	mean
S. tuberosum	Ailsa	681	721	699	700	3210	3281	3182	3224
	Cara	597	646	594	612	3357	3490	3300	3383
	Maris Piper	637	674	569	627	2997	3056	2453	2836
	Pentland Dell	634	604	723	654	2984	2932	3139	3019
LSD ($P < 0.05$)			110.7[a]		63.9[b]		503.6[a]		290.8[b]
date mean		637	661	646		3137	3190	3019	
LSD ($P < 0.05$)			55.3[c]				251.8[c]		
species mean					648				3115
S. phureja	DB 257/28	859	949	863	890	3874	4372	3879	4042
	DB 333/16	697	797	765	753	3771	4178	3807	3919
	DB 337/37	817	823	730	790	3728	3637	3338	3568
	DB 358/23	1032	1188	1099	1106	4522	5164	4602	4763
LSD ($P < 0.05$)			110.7[a]		63.9[b]		503.6[a]		290.8[b]
date mean		851	939	864		3974	4338	3907	
LSD ($P < 0.05$)			55.3[c]				251.8[c]		
species mean					885				4073
LSD ($P < 0.05$)					31.9[d]				145.4[d]
overall date mean		744	800	755		3556	3764	3463	
LSD ($P < 0.05$)			39.1[e]				178.1[e]		

[a] Least significant difference between genotypes at each date within given species. [b] Least significant difference between genotype means averaged over all dates within given species. [c] Least significant difference between date means averaged over all genotypes within given species. [d] Least significant difference between species means averaged over all genotypes and dates. [e] Least significant difference between overall date means averaged over all genotypes and species.

tively by two-dimensional thin-layer chromatography (2D TLC; first direction, chloroform/methanol/water, 75:25:2.5, by vol; second direction, chloroform/methanol/water/acetic acid, 80:9:12:2, by vol) on glass plates of silica gel 60 (20 × 20 cm, 0.25 mm thick, Merck). Components were detected by spraying with primulin (0.01%, w/v, in acetone/water, 60:40, v/v) and observing under UV light. Spots were scraped off the plates, methyl heneicosanoate (5.1 mg in 25 mL of methanol; 100 μL) was added, and direct transesterification in methanolic sulfuric acid and analysis of the released FAME by GC were carried out as described above.

Analytical 2D TLC separations were performed on 10 × 10 cm aluminum-backed silica gel 60 F_{254} plates (Merck) using the same solvent system as above. Plates were sprayed with phosphomolybdic acid (20% w/v in ethanol) followed by charring (150 °C for 10 min) to reveal all lipids. Lipids were identified by running appropriate standards and by the use of specific spray reagents including α-naphthol sulfuric acid reagent [15% (w/v) α-naphthol in 95% ethanol (10.5 mL), 98% (w/v) sulfuric acid (6.5 mL), 95% ethanol (40.5 mL), water (4 mL); heat at 110 °C for 5 min] for sugar groups, ninhydrin reagent (0.2% ninhydrin in water-saturated butan-1-ol, w/v; heat at 110 °C for 10 min) for amino groups, and Phospray (Supelco, Sigma-Aldrich, Poole, U.K.) for phosphate groups.

Statistical Analysis. Treatments were compared by analysis of variance (ANOVA), and GC profiles were summarized by principal components. All analyses were carried out using Genstat for Windows, 6th ed.

RESULTS AND DISCUSSION

Dry Matter Content. Tubers from four *S. tuberosum* cultivars (Ailsa, Cara, Maris Piper, and Pentland Dell) and four *S. phureja* genotypes (DB 257/28, DB 333/16, DB 337/37, and DB 358/23) were sampled in duplicate at each of three storage times (4, 10, and 21 weeks postharvest, corresponding to 0, 6, and 17 weeks of storage at 4 °C). The dry matter content of *S. tuberosum* ranged from 18.1% for Cara to 21.7% for Ailsa (for means of all dates) and from 19.2% for DB 333/16 to 23.2% for DB 358/23 for *S. phureja*. Over all genotypes and dates, *S. phureja* (21.7%) had a small but significantly higher dry matter content than *S. tuberosum* (20.9%). The dry matter content tended to increase slightly with storage time (increase from 20.9% at 4 weeks postharvest to 21.8% at 21 weeks for means averaged over all genotypes and species).

Total Fatty Acid Content in *S. phureja* and *S. tuberosum*. When data were averaged across all genotypes and storage dates, total fatty acid content was significantly higher in *S. phureja* (37% greater) compared to *S. tuberosum* (**Table 1**). This is true whether data are expressed on a fresh (885 compared to 648 μg g^{-1}) or dry weight (4073 compared to 3115 μg g^{-1}) basis.

Within species there was also variation between genotypes. Within *S. tuberosum*, Ailsa had the highest fatty acid content on a fresh weight basis (700 μg g^{-1}), but the levels in Cara (3383 μg g^{-1}) were comparable to those in Ailsa (3224 μg g^{-1}) on a dry weight basis. The levels in Maris Piper (627 μg g^{-1} of fresh weight) and Pentland Dell (654 μg g^{-1}) were higher than those previously reported (496 and 415 μg g^{-1} of fresh weight, respectively) (*10*). This may reflect environmental differences in growing conditions and/or in postharvest storage between the two studies. Additionally, differences in analytical methodology (direct transesterification of freeze-dried material in the present study compared with extraction of lipids from fresh material followed by formation of FAME in the other study) may have contributed toward the discrepancies. The range of values was greater for *S. phureja* genotypes, with DB 358/23 having the highest levels on fresh (1106 μg g^{-1}) and dry weight (4763 μg g^{-1}) bases, whereas the lowest values (753 μg g^{-1} of fresh weight and 3568 μg g^{-1} of dry weight) were found in DB 333/16 and DB 337/37, respectively.

Fatty Acid Compositions of *S. phureja* and *S. tuberosum*. Fatty acids were identified on the basis of GC retention times compared to those of standards and by GC-MS of the methyl esters and DMOX derivatives. The positions of double bonds were confirmed from the mass spectra of the DMOX derivatives (*11*, *12*). The fatty acid compositions (as percent of total fatty acids) of all eight cultivars and genotypes after all storage times were broadly similar (**Tables 2** and **3**). The major fatty acids were 18:2($n-6$) (43−53%), 18:3($n-3$) (16−26%), *n*-16:0 (18−21%), and *n*-18:0 (4−6%) in order of decreasing abundance, similar to that reported by Galliard (*10*).

Table 2. Fatty Acid Composition (Percent Total Fatty Acid) of Tubers from Four Genotypes from Each of the Two Potato Species, *S. tuberosum* and *S. phureja*, at 4 Weeks Postharvest

	S. tuberosum					*S. phureja*					LSD[a] (sig)
fatty acid	Ailsa	Cara	Maris Piper	Pentland Dell	mean	DB 257/28	DB 333/16	DB 337/37	DB 358/23	mean	($P < 0.05$)
n-14:0	0.3	0.3	0.3	0.3	0.3	0.3	0.4	0.4	0.3	0.3	– (NS)
n-15:0	0.3	0.2	0.2	0.2	0.3	0.3	0.3	0.2	0.2	0.3	– (NS)
n-16:0	19.8	18.5	20.3	18.7	19.3	19.8	19.4	19.0	18.7	19.2	– (NS)
16:1(*n*–10)	0.2	0.2	0.1	0.2	0.2	0.1	0.1	0.2	0.1	0.1	0.06 (*)
16:1(*n*–7)	0.2	0.1	0.2	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.02 (**)
i-17:0	0.3	0.2	0.3	0.3	0.3	0.5	0.2	0.8	0.7	0.5	0.06 (***)
n-17:0	0.3	0.3	0.3	0.3	0.3	0.3	0.3	0.2	0.2	0.3	– (NS)
n-18:0	3.9	5.6	5.3	5.4	5.0	3.9	3.9	3.8	3.5	3.7	0.14 (***)
18:1(*n*–9)	0.7	0.8	0.8	0.9	0.8	1.4	0.9	1.1	1.1	1.1	0.24 (**)
18:1(*n*–7)	0.7	0.7	0.8	0.7	0.7	0.6	0.5	0.6	0.6	0.6	0.04 (***)
18:2(*n*–6)	50.1	49.6	50.2	49.2	49.7	53.0	48.0	50.8	48.9	50.2	– (NS)
18:3(*n*–3)	19.5	19.2	16.5	19.0	18.6	15.6	21.9	18.9	22.4	19.7	1.08 (*)
n-20:0	2.0	2.2	2.2	2.3	2.2	2.0	2.0	1.9	1.6	1.8	0.13 (***)
20:2(*n*–6)	0.2	0.1	0.2	0.1	0.1	0.2	0.2	0.2	0.1	0.1	– (NS)
n-22:0	0.5	0.7	0.7	0.7	0.7	0.8	0.8	0.7	0.7	0.7	– (NS)
22:1(*n*–9)	0.2	0.2	0.3	0.1	0.2	0.3	0.1	0.2	0.1	0.2	– (NS)
n-24:0	1.1	1.2	1.5	1.5	1.3	1.1	1.2	1.0	0.9	1.1	0.11 (***)

[a] Least significant difference between species means. Significance levels: NS, not statistically significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

Table 3. Fatty Acid Composition (Percent Total Fatty Acid) of Tubers from Four Genotypes from Each of the Two Potato Species, *S. tuberosum* and *S. phureja*, Averaged over All Storage Times

	S. tuberosum							*S. phureja*							LSD[d]	
fatty acid	Ailsa	Cara	Maris Piper	Pentland Dell	LSD[a]	T × G[b]	mean	DB 257	DB 333	DB 337	DB 358	LSD[c]	T × G[b]	mean	(sig)	T × S[e]
n-14:0	0.3	0.3	0.3	0.4	0.06	NS	0.3	0.3	0.4	0.4	0.4	0.06	NS	0.4	0.03 (***)	*
n-15:0	0.3	0.3	0.2	0.3	0.04	NS	0.3	0.3	0.3	0.3	0.3	0.04	NS	0.3	0.02 (**)	NS
n-16:0	19.4	18.6	20.1	18.0	0.80	NS	19.0	20.0	19.9	19.1	19.5	NS	NS	19.6	0.40 (**)	*
16:1(*n*–10)	0.2	0.2	0.2	0.2	NS	NS	0.2	0.1	0.1	0.2	0.1	NS	NS	0.10	0.01 (***)	NS
16:1(*n*–7)	0.2	0.1	0.1	0.2	0.02	NS	0.1	0.1	0.1	0.1	0.1	NS	NS	0.1	0.01 (***)	NS
i-17:0	0.3	0.2	0.2	0.3	0.04	NS	0.2	0.5	0.1	0.8	0.8	0.04	NS	0.5	0.02 (***)	NS
n-17:0	0.3	0.3	0.3	0.3	0.02	NS	0.3	0.3	0.3	0.3	0.3	0.02	NS	0.3	0.01 (***)	NS
n-18:0	3.9	5.9	5.7	5.7	0.22	**	5.3	4.0	4.0	3.9	3.6	0.22	NS	3.9	0.11 (***)	NS
18:1(*n*–9)	0.6	0.7	0.7	0.9	NS	NS	0.7	1.4	1.0	0.9	1.1	0.18	*	1.1	0.09 (***)	NS
18:1(*n*–7)	0.7	0.7	0.8	0.7	0.04	NS	0.7	0.6	0.5	0.6	0.6	0.04	NS	0.6	0.02 (***)	NS
18:2(*n*–6)	48.2	46.5	48.1	45.8	0.81	NS	47.1	49.0	46.0	48.9	46.2	0.81	*	47.5	– (NS)	NS
18:3(*n*–3)	22.0	21.6	18.1	22.8	1.20	NS	21.1	19.0	23.0	20.4	23.7	1.20	NS	21.5	– (NS)	NS
n-20:0	2.0	2.2	2.3	2.2	0.12	NS	2.2	2.0	1.9	1.9	1.6	0.12	NS	1.8	0.06 (***)	NS
20:2(*n*–6)	0.2	0.1	0.1	0.1	0.08	NS	0.1	0.1	0.2	0.1	0.1	NS	NS	0.1	– (NS)	NS
n-22:0	0.6	0.9	0.8	0.8	0.10	NS	0.8	0.9	0.9	0.8	0.7	0.10	NS	0.8	0.05 (*)	NS
22:1(*n*–9)	0.1	0.2	0.3	0.0	0.13	NS	0.2	0.3	0.1	0.2	0.1	NS	NS	0.2	– (NS)	NS
n-24:0	1.1	1.4	1.7	1.6	0.12	NS	1.4	1.2	1.3	1.1	1.0	0.12	NS	1.2	0.06 (***)	NS

[a] Least significant difference ($P < 0.05$) between *S. tuberosum* genotypes averaged over all storage times. [b] Significance of interaction term between storage time (T) and genotype (G) within specified species. Significance levels: NS, not statistically significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. [c] Least significant difference ($P < 0.05$) between *S. phureja* genotypes averaged over all storage times. [d] Least significant difference ($P < 0.05$) and level of significance between species means averaged over all storage times. [e] Significance of interaction term between storage time (T) and species (S) means.

Galliard (*10*) also reported the presence of 16:1($n-7$) and 18:1($n-9$) as significant minor fatty acids. 16:1($n-7$) was reported at a level of 4% in Pentland Dell, but levels of only 0.2% were detected in our study [even considering that the poorer resolution of packed columns may not have separated the 16:1 isomers, the total 16:1 isomers [16:1($n-7$) plus 16:1($n-10$)] was not greater than 0.4% in our study]. Unusually, one of the 16:1 acids had a double bond in the Δ6-position [the mass spectrum of the DMOX derivative gave a characteristic ion at *m*/*z* 167 for a Δ6 double bond (*12*)]. Traces of an equally unusual 15:1($n-10$) acid suggested a biosynthetic link.

Several other minor fatty acids, not mentioned by Galliard (*10*), were detected in both species. The presence of *i*-17:0 is noteworthy. It was found at low levels in the polar lipids of potato tubers (see below). Branched-chain fatty acids including *i*-17:0 are common components of animals (*13*) and Gram-positive bacteria (*14*) but are rare in plants. Branched-chain acids, including *i*-17:0, have been detected as free fatty acids in potato leaf waxes (T. Shepherd, personal communication), and *ai*-17:0 has been detected as a minor acid in the seed oil of Pinaceae species (*15*). Bacterial contamination is one possible explanation for the presence of *i*-17:0 in the present study, but other typical bacterial fatty acids, such as cyclopropyl acids, were not detected. Also, there was a definite difference in the amount of *i*-17:0 between the two species of potato. Trace amounts of other acids (*i*-15:0, 17:1, 17:2, *n*-21:0, and *n*-23:0) were also detected. Straight-chain saturated fatty acids of chain length greater than *n*-24:0 (*n*-25:0, *n*-26:0, and *n*-28:0), possible components of waxes, were also detected by GC-MS.

There were only minor differences in fatty acid composition between the two species (**Tables 2** and **3**). However, some significant differences were apparent in some of the relatively minor fatty acids that were consistent at all storage times. *S. phureja* (averaged over all genotypes) had higher percentages

Table 4. Linoleic and α-Linolenic Acid Contents of Tubers from Four Genotypes from Each of the Two Species, *S. tuberosum* and *S. phureja*, at 4, 10, and 21 Weeks Postharvest

		μg g^{-1} of freeze-dried matter								
		linoleic acid (18:2)			α-linolenic acid (18:3)			combined (18:2 plus 18:3)		
species	genotype	4 weeks	10 weeks	21 weeks	4 weeks	10 weeks	21 weeks	4 weeks	10 weeks	21 weeks
S. tuberosum	Ailsa	1600	1558	1480	618	735	745	2218	2293	2225
	Cara	1658	1600	1449	636	777	748	2294	2376	2198
	Maris Piper	1499	1472	1115	486	588	442	1984	2060	1558
	Pentland Dell	1461	1327	1342	560	682	797	2021	2009	2139
species mean		1555	1489	1347	575	695	683	2129	2184	2030
LSD[a] ($P > 0.05$)			115.9			76.2			NS	
S. phureja	DB 257/28	2042	2099	1766	595	866	813	2638	2965	2579
	DB 333/16	1802	1896	1685	812	972	879	2614	2868	2564
	DB 337/37	1887	1768	1571	695	754	705	2582	2523	2275
	DB 358/23	2203	2354	2010	998	1238	1105	3201	3592	3116
species mean		1983	2029	1758	775	958	876	2759	2987	2633
LSD[a] ($P > 0.05$)			115.9			76.2			217.4	

[a] Least significant difference between species means at each storage time.

of *i*-17:0 and 18:1(*n*−9) and lower percentages of *n*-18:0, *n*-20:0, *n*-24:0, and 18:1(*n*−7). Considering the values averaged over all storage times (**Table 3**), it is worth noting that for some fatty acids [e.g., 16:1(*n*−7)] there were statistically significant differences between the mean values for both species, although the differences were actually extremely small. This is partly due to the high precision of the method and partly to the large number of data points (and therefore high degrees of freedom) in this data set. Such differences are not considered as being important.

To gain further insights into those fatty acids that are most significant in separating the two species, a principal component analysis (PCA) was carried out on all samples for all 17 fatty acid variables. The application of PCA is relevant when the data consist of many variables, and it is desirable to reduce the number of variables to a manageable level without removing too much of the relevant variation in the data. New variables, called components, are created from weighted averages of the original variables. The values, or scores, of these new components can be determined for each sample by summing the products of the values of the original variables and the weights or loadings. The components have two important properties. First, they are all uncorrelated with each other, and second, the variance of the first component is greater than the variance of the second component, and so on. Thus, it can be stated that the first principal component, for example, accounts for *x*% of the total variation in the data. If samples or groups of samples are separated by a particular component (i.e., according to their scores), then the original variables that have the greatest influence on that separation tend to be those with the largest loadings for that component. Loadings can have positive or negative values, and variables with large loadings of the same sign tend to be positively correlated, whereas those with opposite signs tend to be negatively correlated.

Principal component 1 (PC1) accounted for 24% of the total variation and, to a large extent, separated the two species, as can be seen in the plot of PC1 against PC2 (**Figure 1a**). The loading plot for PC1 confirmed the importance of *i*-17:0, *n*-18:0, *n*-20:0, *n*-24:0, 18:1(*n*−7), and 18:1(*n*−9), to a lesser degree, in achieving the separation. Ailsa was the only *S. tuberosum* cultivar that did not clearly separate from the *S. phureja* genotypes by PC1. Indeed, Ailsa stood out from the other *S. tuberosum* cultivars in containing lower levels of saturated fatty acids, especially *n*-18:0, *n*-20:0, and *n*-24:0. There was an indication that Ailsa was grouping with the other *S. tuberosum* cultivars when PC1 was plotted against PC3 (**Figure 1b**; PC3 accounts for 14% of the total variation).

There was comparatively little variation in the fatty acid composition within individual species, although some statistically significant differences were observed (**Table 3**). For example, within *S. phureja*, DB 333/16 had a lower percentage of *i*-17:0, whereas the lowest 18:2(*n*−6) and highest 18:3(*n*−3) values were observed in DB 333/16 and DB 358/23. Within *S. tuberosum*, *n*-18:0 was consistently lowest in the cv. Ailsa, whereas the levels of 18:2(*n*−6) were significantly lower in Cara and Pentland Dell compared with the other cultivars.

Absolute Levels of Linoleic and α-Linolenic Acids in *S. phureja* and *S. tuberosum*. Autoxidation (*16*) and enzymic (hydroperoxide lyase) (*17*) action on hydroperoxides derived from18:2(*n*−6) and 18:3(*n*−3) fatty acids produce a range of flavor-active volatile aldehydes, ketones, alcohols, and alkyl furans. The absolute levels (μg g^{-1} of freeze-dried matter) of both 18:2(*n*−6) and 18:3(*n*−3) were higher in the *S. phureja* genotypes than the *S. tuberosum* cultivars (**Table 4**), and therefore in *S. phureja* there is more substrate for fatty acid derived flavor compounds that increase upon cooking, presumably by autoxidation and/or enzymic processes. This may partially explain the difference in flavor attributes between the two species (*2*). Notably, *S. phureja* had a more intense earthy flavor, and it may be speculated that this characteristic could have arisen from 4*Z*-heptenal, a compound found in boiled potatoes, derived from an oxidation product (2*E*,6*Z*-nonadienal) of α-linolenic acid, and considered to impart an earthy flavor (*6*). Differences in lipoxygenase and/or hydroperoxide lyase activity may also be important factors in determining the levels of flavor volatiles (assuming that these enzymes are active during cooking). However, it should be borne in mind that differences in volatile compounds derived from non-lipid precursors (e.g., amino acids and sugars) have also been observed between the two species (unpublished data) and may also have a significant effect on the flavor attributes.

Effect of Tuber Storage on Total Fatty Acid Content, Fatty Acid Compositions, and Absolute Levels of Linoleic and α-Linolenic Acids in *S. phureja* and *S. tuberosum*. The total fatty acid contents of the tubers, on wet and dry weight bases, remained reasonably constant with storage time. Averaged over all species and genotypes there was a small but statistically significant increase after 10 weeks postharvest, but after 21 weeks the level decreased to a value close to the initial value at 4 weeks postharvest (**Table 1**). This trend was more evident

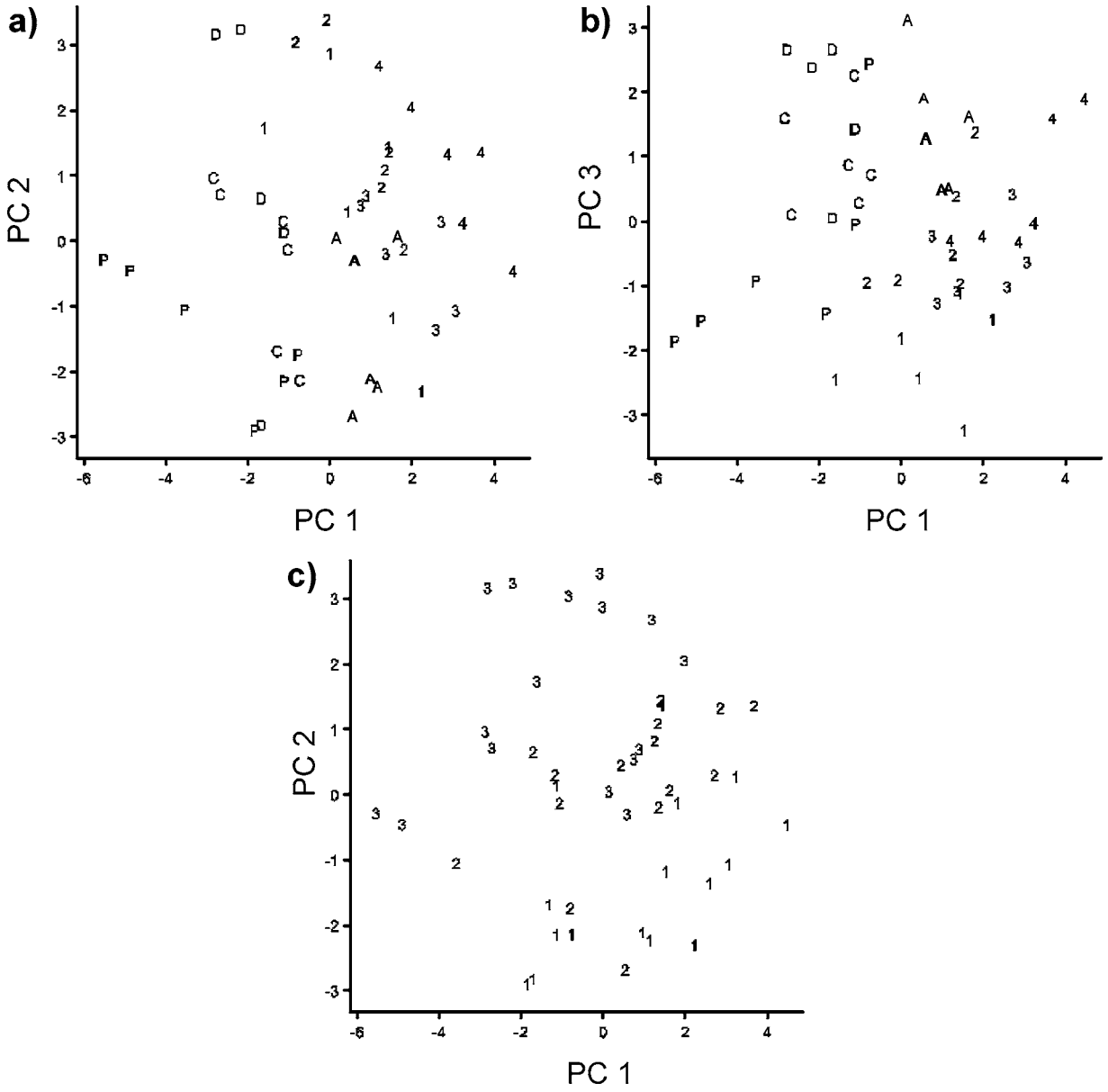

Figure 1. Score plots from principal component analysis of all 17 fatty acids for all genotypes of both species at all three storage dates: (**a**) plot of PC1 against PC2 with samples labeled according to genotype or cultivar; (**b**) plot of PC1 against PC3 with samples labeled according to genotype or cultivar; (**c**) plot of PC1 against PC2 with samples labeled according to storage time. A, Ailsa; C, Cara; D, Pentland Dell; P, Maris Piper; 1, DB 257/28; 2, DB 333/16; 3, DB 337/37; 4, DB 358/23; 1, 4 weeks postharvest; 2, 10 weeks postharvest; 3, 21 weeks postharvest.

for *S. phureja* than for *S. tuberosum*, for which differences with storage were not statistically significant. Similar trends were reported earlier for the total lipid content of tubers stored at 3 °C (*18*), 4 °C (*19*), and 5 °C (*20*, *21*). The trend can largely be accounted for by changes in the levels of the major fatty acids 18:2(*n*−6) and 18:3(*n*−3), the sum of which (**Table 4**) showed trends similar to those for the total fatty acids, and possible explanations for these changes are discussed below.

When the changes in percent fatty acid composition with storage were considered, the overall mean values of both species were compared because, with the exceptions of the fatty acids *n*-14:0 and *n*-16:0, there was no statistically significant interaction between storage date and species (**Table 5**). There were only small variations in the percent fatty acid composition with storage, as observed previously (*20*, *21*). There was a small, but statistically significant, decrease in 18:2(*n*−6) and an increase in 18:3(*n*−3) [the change in 18:3(*n*−3) from 10 to 21 weeks postharvest was not significant], a trend previously observed for tubers stored at 5 °C over a period similar to that of the present study (*21*), at 4 °C for several months (*22*) and at 20 °C (*21*) and 21 °C (*23*). Under storage conditions similar to those of the present study, Schwartz et al. (*24*) observed a similar trend for 18:3(*n*−3), but the pattern was less clear for 18:2(*n*−6). In another study (*25*), after 16 weeks storage at 4 °C, greater changes in 18:2(*n*−6) and 18:3(*n*−3) (and an increase in *n*-16:0) than those in the present study were observed for one variety, but for another variety a different trend was evident [18:3(*n*−3) decreased and 18:2(*n*−6) remained unchanged]. Similar to the present study, the ratio of 18:3(*n*−3) to 18:2(*n*−6) increased up to ∼20 weeks of storage when tubers were kept at 3 °C (*18*). It was suggested that increased fatty acid unsaturation may be a response to low temperatures to maintain membrane fluidity. Also, in the present study, in agreement with earlier studies (*20*, *21*, *23*), but contrary to another (*24*), the sum of 18:2(*n*−6) and 18:3(*n*−3) was conserved.

A PCA of all the data revealed that PC2 accounted for 17% of the total variation, and substantial separation according to

Table 5. Effect of Storage on the Fatty Acid Composition (Percent Total Fatty Acid) of Tubers, Averaged over All Genotypes and Species

fatty acid	postharvest storage 4 weeks	10 weeks	21 weeks	LSD[a] ($P < 0.05$)	T × S[b]
n-14:0	0.3	0.4	0.4	NS	*
n-15:0	0.3	0.3	0.3	0.02	NS
n-16:0	19.3	18.9	19.7	0.49	*
16:1(*n*–10)	0.1	0.1	0.2	NS	NS
16:1(*n*–7)	0.1	0.1	0.2	0.01	NS
i-17:0	0.4	0.4	0.4	NS	NS
n-17:0	0.3	0.3	0.3	0.01	NS
n-18:0	4.4	4.6	4.8	0.14	NS
18:1(*n*–9)	1.0	0.9	0.9	NS	NS
18:1(*n*–7)	0.6	0.6	0.7	0.03	NS
18:2(*n*–6)	50.0	47.0	45.1	0.50	NS
18:3(*n*–3)	19.1	22.1	22.6	0.73	NS
n-20:0	2.0	2.0	2.0	NS	NS
20:2(*n*–6)	0.1	0.1	0.1	0.05	NS
n-22:0	0.7	0.8	0.9	0.06	NS
22:1(*n*–9)	0.2	0.1	0.2	NS	NS
n-24:0	1.2	1.3	1.4	0.07	NS

[a] Least significant difference. [b] Significance of interaction term between storage time (T) and species (S). Significance levels: NS, not statistically significant; *, $P < 0.05$.

Table 6. Polar Lipid Composition and Content in Tubers from the Cultivar Cara (*S. tuberosum*) and the Genotype DB 333/16 (*S. phureja*)

lipid	polar lipid composition (mol %) DB 333/16	Cara	probability[a]	polar lipid content (nM g^{-1} of fresh wt) DB 333/16	Cara	probability[a]
MGDG	9.2	8.7	0.281	106	81	0.056
DGDG	14.3	12.2	0.059	164	113	0.025
SQDG	1.7	1.4	0.167	19	13	0.083
PC	29.9	30.7	0.386	342	285	0.041
PE	16.4	19.6	0.192	188	182	0.654
PG	2.1	1.2	0.092	24	11	0.062
PI	9.3	9.3	0.985	107	87	0.338
PS	1.0	1.5	0.181	12	14	0.331
DPG	0.8	0.7	0.314	9	6	0.047
PA	3.5	3.2	0.421	41	30	0.179
ASG	8.4	9.0	0.566	97	83	0.367
lipid A	0.7	0.8	0.697	9	8	0.615
lipid B	2.0	1.1	0.034	23	10	0.008
lipid C	0.6	0.6	0.251	7	6	0.218
total				1147	929	0.062

[a] *F* probability value from ANOVA for comparison of varietal means.

storage date was achieved (**Figure 1c**). Samples taken at 4 and 21 weeks postharvest were separated, and those at 10 weeks were intermediate in position but overlapped with the other two groups. The loading plot for PC2 confirmed the important influence of 18:2(*n*−6) and 18:3(*n*−3) in achieving the separation.

In both species, there were small but statistically significant changes in the absolute levels (in μg g^{-1} of freeze-dried matter) of 18:2(*n*−6) and 18:3(*n*−3) with storage (**Table 4**). 18:2(*n*−6) decreased with storage time from 4 to 21 weeks postharvest, but the levels were essentially unchanged between 4 and 10 weeks. On the other hand, the levels of 18:3(*n*−3) increased between 4 and 10 weeks but after 21 weeks had stabilized in *S. tuberosum* and showed a slight statistically significant decrease in *S. phureja*. These patterns can obviously not be explained by an increase in autoxidation with storage time, as 18:3(*n*−3) would have decreased. In fact, 18:3(*n*−3) is more susceptible to oxidation than 18:2(*n*−6), due to the greater degree of unsaturation (*26*). Presumably the changes in 18:2(*n*−6) and 18:3(*n*−3) levels are due to differences in the metabolism of the two types of fatty acids and may simply be a response to the low storage temperature to maintain membrane fluidity. However, these fatty acids are precursors of a range of oxylipins that have biological activity, notably in plant defense mechanisms (*27*), and the changes may be related, at least partly, to differential rates of oxylipin production from the two fatty acids. Oxylipins are derived enzymically from hydroperoxides that are produced by the action of lipoxygenases on free fatty acids, which in turn are derived from complex lipids such as phosphatidylcholine. The major lipoxygenase in potato tuber (Lox1) preferentially uses 18:2(*n*−6) as a substrate (*28*), which would be consistent with the observations in our study. Additionally, a decrease in the amount of 18:2(*n*−6) in complex lipids has been observed after tuber storage, together with an increase in the oxylipin, colneleic acid, and its precursor the 9-hydroperoxide of 18:2(*n*−6) (*29*).

Polar Lipids. The polar lipids of one representative of *S. tuberosum* (Cara) and *S. phureja* (DB 333/16) were qualitatively similar, and only minor differences were apparent in the percent compositions (**Table 6**). Phosphatidylcholine (PC) was the major lipid followed by phosphatidylethanolamine (PE) and digalactosyldiacylglycerol (DGDG). Phosphatidylinositol (PI), monogalactosyldiacylglycerol (MGDG), and acyl sterol glycoside (ASG) were the next most abundant lipids, and phosphatidic acid (PA), sulfoquinovosyldiacylglycerol (SQDG), phosphatidylglycerol (PG), phosphatidylserine (PS), diphosphatidylglycerol (DPG), and three unidentified lipids (A−C) were minor components. The unknown lipid A was identified as a glycolipid, and its low R_f value suggested that it may be the polygalactosyldiacylglycerol identified by Galliard (*30*). No further structural information was obtained with respect to the characterizations of the unidentified polar lipids A−C. Sterol glycosides and ceramides were also detected in both species, but they were not quantified.

The relative abundances of the lipids in both potato species were similar to that observed in *S. tuberosum* (var. Majestic) by Galliard (*30*). On a mole percent composition basis, with the exception of lipid B, there was no statistically significant difference (at the 95% significance level) between the profiles of the two species (**Table 6**). This may be partly due to the low number of degrees of freedom in the statistical test (ANOVA) used. However, considering *F* probability values of <0.1 (i.e., 90% significance level), there were indications in the data that on a mole percent composition basis DGDG, PG, and lipid B were higher in the *S. phureja* genotype DB 333/16. On a mole per wet weight basis, at the 90% significance level, the total amount of polar lipids was higher in DB333/16. DGDG, PC, DPG, and lipid B were higher (95% level) in DB 333/16, and there were suggestions that MGDG, SQDG, and PG were also higher (90% level) in this genotype (**Table 6**). The higher levels of polar lipids in DB333/16 as compared with the *S. tuberosum* cv. Cara are not surprising considering the higher levels of total fatty acids (**Table 1**), the majority of which will be components of polar lipids. It is worth noting that the total fatty acid levels were higher in other *S. phureja* genotypes compared with DB 333/16, and therefore it would be expected that the levels of polar lipids would also be higher.

The fatty acid profiles of each lipid class were essentially similar between the two species and showed the same characteristics as those reported earlier for *S. tuberosum* (*23*, *30*) (**Table 7**). The galactolipids MGDG and DGDG contained relatively high proportions of 18:3(*n*−3), as did DPG, and

Table 7. Fatty Acid Composition (Percent Total Fatty Acids)[a] of Individual Polar Lipid Classes in Tubers from the Cultivar Cara (*S. tuberosum*) and the Genotype DB 333/16 (*S. phureja*)

		fatty acid					
lipid	genotype	*n*-16:0	*n*-18:0	18:1[b]	18:2(*n*–6)	18:3(*n*–3)	*n*-20:0–24:0
MGDG	Cara	2	1	1	55	40	<1
	DB 333/16	5	2	1	53	39	<1
DGDG	Cara	10	8	2	52	26	2
	DB 333/16	12	7	1	53	26	1
SQDG	Cara	28	9	2	41	19	1
	DB 333/16	32	7	<1	41	19	<1
PC	Cara	18	6	2	53	19	2
	DB 333/16	22	5	2	53	17	1
PE	Cara	20	6	1	54	15	4
	DB 333/16	21	4	1	57	14	3
PG	Cara	50	8	5	28	8	1
	DB 333/16	58	4	2	27	8	<1
PI	Cara	39	5	1	35	19	1
	DB 333/16	40	4	1	35	19	1
PS	Cara	5	8	2	32	12	42
	DB 333/16	2	8	<1	34	11	45
DPG	Cara	8	2	4	54	32	0
	DB 333/16	8	2	3	53	33	<1
PA	Cara	20	6	2	50	15	6
	DB 333/16	21	4	2	53	17	2
ASG	Cara	44	15	1	23	6	11
	DB 333/16	53	10	1	22	5	9

[a] Fatty acid percentages are means of duplicate analyses. [b] 18:1 is the sum of 18:1(*n*–9) and 18:1(*n*–7).

MGDG was particularly low in *n*-16:0. PC and PE had similar profiles with a substantially higher percentage of 18:2(*n*−6) than 18:3(*n*−3) and *n*-16:0, and PI and PG, together with acyl sterol glycoside and to a lesser extent SQDG, had relatively high levels of *n*-16:0. The fatty acid composition of PS had not been previously reported in potato tubers, but similar to the composition of other plant PS (*31*), there were characteristically high proportions of long-chain fatty acids, especially *n*-20:0.

Detailed information on the molecular species compositions of individual polar lipids of the two species could be obtained by taking a "lipodomics" approach, to give further information on, for example, the effects of tuber storage. It has previously been found that changes in the levels of microsomal 18:2(*n*−6)- and 18:3(*n*−3)-bearing species with storage at 4 °C vary for different polar lipid classes (*32*). There was an increase in the levels of 18:3(*n*−3)-bearing species and a decrease in 18:2(*n*−6)-bearing species in PC and PE, whereas most molecular species declined in DGDG and MGDG. However, these changes occurred over much longer storage periods (up to 38 months) than in the present study, and it is not possible to deduce what might be happening over shorter storage periods (up to ∼4 months).

Currently we are using a metabolomics approach to look at the polar and nonpolar metabolites, and the volatile compositions, of the two species, with a view to highlighting other differences between the species and to further our understanding of the processes involved in determining the differences in flavor characteristics between the two species.

Conclusions. The major finding of the study was that, on the basis of the analysis of four genotypes/cultivars of each species, the diploid *S. phureja* had higher total fatty acid levels than the tetraploid *S. tuberosum*. There were only small differences in fatty acid composition between the two species, although some differences [*i*-17:0, 18:1(*n*−7), 18:1(*n*−9), *n*-18:0, *n*-20:0, and *n*-24:0] were statistically significant. Averaged over all species and genotypes, the total fatty acid content initially increased with storage (from 4 to 10 weeks postharvest) at 4 °C but then decreased to the initial levels (after 21 weeks). A similar pattern was apparent for *S. phureja* but not for *S. tuberosum*, when the mean values of the genotypes and cultivars, respectively, were considered. Biologically, 18:2(*n*−6) and 18:3(*n*−3) are the most important fatty acids because they are the precursors of oxylipins. In both species there were small but statistically significant changes in 18:2(*n*−6) and 18:3(*n*−3) levels with storage. Over the whole storage period, 18:2(*n*−6) decreased and 18:3(*n*−3) increased, and it is speculated that these changes may be related to oxylipin metabolism and/or a response to the low storage temperature to maintain membrane fluidity. The levels of 18:2(*n*−6) and 18:3(*n*−3) were higher in *S. phureja* than in *S. tuberosum*, and it is possible that this may partly explain the differences in flavor characteristics between the two species. The polar lipids of one representative of *S. tuberosum* (Cara) and *S. phureja* (DB 333/16) were qualitatively similar, and there were only minor differences in the percentage compositions and in the fatty acid compositions of the individual lipids. Complimentary to the differences in total fatty acid levels between the two species, the levels of total polar lipids, and of some individual lipids, were higher in *S. phureja* compared with *S. tuberosum*.

The findings of this study would at present have no influence on potato-breeding programs. However, there is a requirement for markers of a variety of characteristics, including flavor. As more information becomes available on the links between tuber fatty acids or lipids and flavor, there is the possibility that the content of specific fatty acids or lipids in raw tubers may be used as markers for flavor characteristics (favorable or detrimental) of cooked potatoes.

ABBREVIATIONS USED

ASG, acyl sterol glycoside; DGDG, digalactosyldiacylglycerol; DMOX, dimethyloxazoline; DPG, diphosphatidylglycerol; FAME, fatty acid methyl esters; GC, gas chromatography; GC-MS, gas chromatography−mass spectrometry; MGDG, monogalactosyldiacylglycerol; PA, phosphatidic acid; PC, phosphatidylcholine; PCA, principal component analysis; PC1, principal component 1; PE, phosphatidylethanolamine; PG, phosphatidylglycerol; PI, phosphatidylinositol; PS, phosphatidylserine; SQDG, sulfoquinovosyldiacylglycerol; TLC, thin-layer chromatography; fatty acid abbreviations are illustrated by the following examples: *n*-14:0, tetradecanoic acid; *i*-17:0, 15-methyl hexadecanoic acid; 18:2(*n*−6), 9*Z*,12*Z*-octadecadienoic acid or linoleic acid.

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