
Solanum tuberosum

Scientific Name

Solanum tuberosum L.

Synonyms

Solanum andigenum Juz. & Bukasov, *Solanum andigenum* subsp. *aya-papa* Bukasov & Lechn., *Solanum andigenum* subsp. *bolivianum* Lechn., *Solanum andigenum* subsp. *ecuatorianum* Lechn., *Solanum aquinas* Bukasov, *Solanum chilense* Berthault, *Solanum chilotanum* Hawkes, *Solanum cultum* Berthault, *Solanum diemii* Brücher, *Solanum fonckii* Phil., *Solanum kesselbrenneri* Juz. & Bukasov, *Solanum leptostigma* Juz. & Buk., *Solanum molinae* Juz., *Solanum oceanicum* Brücher, *Solanum ochoanum* Lechn., *Solanum sanmartiniense* Brucher, *Solanum subandigena* Hawkes, *Solanum tascalense* Brucher, *Solanum tuberosum* var. *guaytecarum* Hawkes, *Solanum tuberosum* var. *tuberosum*, *Solanum tuberosum* subsp. *tuberosum*, *Solanum zykini* Lechn.

Family

Solanaceae

Common/English Names

Common Potato, Irish Potato, European Potato, Potato, Spud, White Potato

Vernacular Names

Afrikaans: Aartappel

Albanian: Patate

Arabic: Batates

Austria: Aardapfel, Ärdäppel, Bramburi, Erdapfel (German)

Bulgarian: Kartof

Burmese: Ah Lou, Ar Loo

Chinese: Ma Ling Shu, Tǔdòu, Yángyù

Croatian: Krumpir

Czech: Brambor

Danish: Kartoffel, Kartoffler

Dutch: Aardappel, Aardappelen

Estonian: Kartul

Ethiopia: Dinitich

Finnish: Peruna, Potaati

French: Pomme De Terre, Patata

Gabon: Émango-a-mutangani (Baduma), Amongo-mbé-ntanga (Bakèlè), Mongu-Bibamba (Balumbu), Mbala-bibamba (Bapunu), Mbala-yi-mutangeni (Bavarama), Bavungu, Eshira), Lifita-la-gibamba (Bavili),

Mbongo-y'utangani (Benga), Imongo-ntangani (Béséki), Amonghe-ntangha (Fang), Futa-wu-otangani (Mindumu), égwéta-a gébamba (Mitsogo), Mongo-y'atanga (Mpongwè, Galoa, Nkomi, Orungu), Mongo-a-gebamba (Ngowé)

German: Herdapfel, Inkatrüffel, Kartoffel, Kartoffeln, Kautüffel, Ketüffel, Krumbirn, Krumbiir, Tartuffli

Greek: Patáta

Hungarian: Burgonya

Icelandic: Kartafla

India: Aalu (Bengali), Bataka, Batata (Gujerati), Alu, Salooalu (Hindi), Urulaikkilangnku (Tamil)

Indonesia: Kentang

Italian: Pomi Di Terra, Patata, Tartufo

Japanese: Jagaimo

Korean: Gamsa

Khmer: Damlong Barang

Laotian: Man Falangx

Latvian: Kartupelis

Malaysia: Ubi Kentang

Morocco: Batâtâ, Btâtâ (Moroco), Pomme De Terre (French)

Nepali: Alu, Aloo

Papua New Guinea: Poteto

Peru: Papa Común

Philippines: Papas, Patatas (Cebu Bisaya, Bikol, Tagalog)

Polish: Ziemniaki

Portuguese: Batata, Batata-Da-Terra-Semelha, Batateira

Romanian: Cartof

Russian: Kartoffel, Kartoška

Serbian: Krompir

Slovakian: Zemiak, Bramboru

Slovenian: Krompir

Spanish: Papa, Patata

Swedish: Jordpäron, Kartoffel, Potatis, Potät, Tartuffe

Switzerland: Ardoffel, Mailinterra, Tartuffel, Tiffel, Truffel (French, Romansh Switzerland), Erdbirne, Erpele, Frundbirne, Gummel (German, Schwyz Canton), Grundbirn, Happere, Hardopfel, Harpfel (German, Upper Valais)

Welsh: Cloron, Tatws

Thai: Man-Farang, Man-Alu

Turkish: Patates

Ukrainian: Kartóplja

Vietnamese: Cây Khoai Tây, Khoai Tay

Origin/Distribution

The potato originated in the Andean regions of Peru and Bolivia. The potato was introduced into Spain from South America in the latter half of the sixteenth century. From Spain, the potato was introduced to adjacent countries and within 100 years was being grown fairly extensively in many regions of Europe. Distribution beyond Europe soon occurred with the introduction into India in the seventeenth century and China and Japan in the eighteenth century.

Agroecology

Potato is a cool climate crop. It prefers day temperatures of 20–25°C and night temperatures below 20 °C. Such temperature conditions are conducive to growth and tuberisation. Night temperatures above 22 °C retard tuberisation. In the tropics it is usually grown in the highlands above 800 m where the temperatures are cooler. In PNG they are grown in altitude between 1500 m and 2200 m. High light intensities are required for optimum dry matter production. It is susceptible to frost and freezing. Potato requires a well distributed rainfall of 500–750 mm in a growing period of 3–4.5 months.

Potato grows on a wide range of soils but not waterlogged soils. It grows best in loose, friable soil and well-drained mineral or organic soils with medium loam or light or medium silty textures. Deep soils with good aeration and permeability give good growth and high tuber yields. Potato tolerates a wide range of pH from 4.8–7.

Edible Plant Parts and Uses

Potato is a very versatile food crop that can be used in multivariate ways. It is eaten cooked and occasionally raw. Potato can be boiled, steamed,

microwaved, baked, fried, grilled, mashed and added to soups, stews, curries, pies, vegetable salads, dumplings, pancakes ('rostiti') and goes well with all sorts of meat and seafood. One common dish is mashed potato where boiled, peeled potato is mashed with butter, margarine, milk or yoghurt. Potato is also consumed as fresh fries, pomes fries, wedges, potato bread (such as boxty) and hash browns. Potato is also thinly sliced and made into chips and crisps by baking or deep-frying for snack appetiser or as a side dish. Potatoes have been used to prepare a product known as chuño, which has played an important role in the diet of the population of the highland and lowland Andes of South America. Potato can be processed into many dehydrated, frozen or canned tubers. Potatoes can also be processed into alcohol and alcoholic beverages including vodka and schnapps.

Potato tuber storage protein, patatin, was found to have potential as food ingredients, in cheese making (Spellbrink et al. 2015). When patatin was added to milk during cheese making, the lipase preferentially released short-chain fatty acids that contributed to cheese flavour in a dose-dependent manner. Fortuitously, the lipase activity was found mainly in the curd.

Potato flour/potato starch is an important processed product from potato and has highly versatile uses in manufacturing convenience foods—ready to cook instant curries, dhals and snacks. Potato flour/starch can be used to prepare potato mash, snack foods, extruded foods, sweets and other bakery products (cakes, bread, pancakes, etc.), weaning foods and baby foods. Its protein content is superior to that of cassava and yam flour, slightly inferior to that of refined maize meal and wheat flour and similar to that of rice. Potato flour has higher levels of fibre than refined wheat flour, maize meal and rice but lower levels of fibre than cassava and yam flour. Its carbohydrate and energy contents are comparable to those of similar foods. The high starch content in potato flour can improve the functional properties of several food products. It has a higher heat point than cornstarch, so it may be superior for certain foods that require high temperatures. Another health benefit is that potato

flour or potato starch is gluten-free and is used as a substitute for wheat to make gluten-free food products for people with gluten intolerance. It can be also blended with wheat flour to make instant noodles, the Indian 'paratha' bread and the Indian sweet preparation 'gulab jamun' (potato flour, wheat flour and milk). It is commonly used as thickeners in soups, sauces and gravies. Potato starch is much used for determining the diastatic value of malt extract (Grieve 1971). A volatile oil—chemically termed amylic alcohol, in Germany known as *Fuselöl*—is distilled by fermentation from potato spirit. Boiled with weak sulphuric acid, potato starch is changed into glucose or grape sugar, which by fermentation yields alcohol, this spirit being often sold under the name of British Brandy.

Potato starch/flour is widely used for making commercial extruded and blended potato chips/crisp snack food, viz. Pringles and Lay's Stax brands.

The carbohydrate (starch and sugar) composition of tubers plays an important role in determining variety usage. Processing varieties, for example, must have relatively high starch and low reducing sugar (glucose/fructose) levels. Starch content is directly related to specific gravity (SG) or dry matter (DM) in tubers. Typically, 60–80 % of the dry matter is present as starch. Therefore, high specific gravity or high dry matter (solids) tubers contain high levels of starch. Generally, table varieties have low SG below 1.069 and low DM below 18.1 %. Some examples are Desiree, Red Pontiac, Sequoia, Sebago, Bintje, Patrones, Denali, Granola, Tess, Pontiac, Bison, Red Bison and Nadine. Varieties with high SG above 1.079 and high DM above 20.3 % are used for processing, e.g. Atlantic, Snowden, Shepody, Niska, Chipeta, Norvalley, Ivory Crisp, Dakota Pearl, Gemchip, Russet Burbank, Ranger Russet and Kennebec.

Botany

An erect or sprawling herb, 30–100 cm tall, with robust angular, branched and winged stem glabrous or sparsely pubescent with simple and

glandular hairs (Plates 1 and 2). Stolons bearing underground tubers; tubers white, brown, yellowish brown, pink, red, purple or purplish blue; globose, oblate or elliptic; 3–10 cm in diameter; fleshy; and with axillary buds (eyes) and numerous lenticels (Plates 3, 4, 5, 6, 7, 8, and 9). Leaves alternate, interruptedly odd-pinnate, with 6–8 pairs of leaflets and smaller, unequal interstitial leaflets; petiole 2.5–5 cm long, leaflet blade ovate



Plate 1 Potato plant habit

or oblong, 2–10 cm by 1–6 cm, dark green, pinnatinerved, mostly sparingly pilose. Inflorescences appearing terminal, leaf opposed, or axillary, many-flowered, sparingly branched panicles. Pedicel articulate near middle, 1–2 cm. Calyx campanulate with 5-lanceolate lobes sparsely pubescent; Corolla white, pink, or blue purple (Plate 2), sometimes all on one plant, rotate to rotate-stellate, 2.5–3 cm in diameter, with 5 deltate lobes, 5 mm; filaments thick with five free, erect yellow anthers, 5–6 mm. Ovary glabrous. Style 8 mm with capitate stigma, berry green or yellowish green, often striped, globose, smooth, 1.5–2 cm in diameter. Seeds numerous (300), flat, suborbicular to ovate, small, yellowish brown embedded in mucilaginous pulp.

Nutritive/Medicinal Properties

The proximate nutrient value per 100 g edible portion of raw, skin potato was reported as: water 83.29 g, energy 58 kcal (243 kJ), protein 2.57 g, total lipid 0.10 g, ash 1.61 g, carbohydrate 12.44 g, total dietary fibre 2.5 g, minerals (Ca 30 mg, Fe 3.24 mg, Mg 23 mg, P 38 mg, K 413 mg, Na 10 g, Zn 0.35 mg, Cu 0.423 mg, Mn 0.602 mg, Se 0.3 µg), vitamins (vitamin C 11.4 mg, thiamine 0.021 mg, riboflavin 0.038 mg, niacin 1.033 mg, pantothenic acid 0.302 mg, vitamin B6 0.239 mg), total folate 17 µg, total saturated fatty acids 0.026 g (10:0 0.001 g, 12:0 0.003 g, 14:0 0.001 g, 16:0 0.016 g, 18:0 0.004 g),

Plate 2 Leaves and flower





Plate 3 Potatoes with different skin colours

Plate 4 Desiree potatoes



total monounsaturated fatty acids 0.002 g (16:1 undifferentiated 0.001 g and 18:1 undifferentiated 0.001 g) and total polyunsaturated fatty acids 0.043 g (18:2 undifferentiated 0.032 g and 18:3 undifferentiated 0.010 g) (USDA-ARS 2014). The variety \times location interaction and location effects of soluble and insoluble dietary

fibre contents of six Canadian potato varieties were significant on a dry weight basis (Mullin et al. 1993). The same effects for total dietary fibre were significant after storage except for soluble fibre in the skins, insoluble fibre in the flesh and whole potatoes. On a fresh weight basis, the range of soluble fibre was 0.9–1.30 % for both

Plate 5 Bintje potatoes**Plate 6** Kipfler potatoes

fresh and stored potatoes; for insoluble fibre the range was 0.6–0.8 % and 0.6–0.7 % for fresh and stored samples, respectively.

The following sugars were found in cold-stored Kennebec potato tubers with stearic acid as internal standard: β -D-fructose; α -glucose, β -D-glucose, myo-inositol and sucrose (Varns and Shaw 1973). Potato tubers were found to contain citric and malic acids in the ratio of nearly 20:1 together with a small amount of isocitric acid (Curl and Nelson 1940).

A total of 17 fatty acids were detected in quantifiable amounts in all genotypes of *Solanum phureja* and *S. tuberosum* (Dobson et al. 2004). The predominant fatty acid was linoleic followed by α -linolenic and palmitic acids. 15-Methyl

hexadecanoate was present as a minor acid in both species. 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. Niacin degradation in potato followed first-order kinetics, where the rate constant increased with an increase in the temperature of 50–120 °C (isothermal process) (Nish et al. 2009). The results obtained indicate a niacin degradation of a similar magnitude in all three modes of cooking, namely, normal open pan cooking, pressure cooking and a newly developed and patented fuel-efficient ‘EcoCooker’. Potatoes had been found to contain a number of health-promoting phytonutrients such as phenolics, flavonoids,

Plate 7 Purple Congo potatoes**Plate 8** Royal blue potatoes

folates, kukoamines and carotenoids (Ezekiel et al. 2013). Pigmented potatoes contained high concentration of phenolic acids as compared to white-fleshed potatoes and richer in natural colourants and antioxidants.

Proteins

Potato had been reported to have several types of protein. Osborne and Campbell (1896) isolated a globulin from potato tubers by salt extraction which they designated 'tuberin'. Kon (1928) reported on the nutritional value of tuberin, the globulin of potato. Groot et al. (1947) separated tuberin into two fractions by electrophoresis. Slack (1948) concluded that the only true protein present in potato was a globulin. Lindner et al. (1960) fractionated potato tuber proteins into

tuberin, globulin II, albumin, prolamine and glutenin. Stegmann and Loeschcke (1961), Desborough and Peloquin (1966) and Nakasone et al. (1972) separated tuber proteins into additional fractions by electrophoresis and chromatography. Kapoor et al. (1975) fractionated protein in Red Pontiac tuber into tuberin, the main proteins (71 %), and found that 40 % of tuberin was albumin. All the protein fractions except prolamine were well balanced in essential amino acids and comparable to FAO reference protein. Methionine was the limiting amino acid of the potato fractions. The chemical score, essential amino acid indices and biological value of albumin, globulin, glutenin and residual protein did not vary significantly. Since all the fractions except prolamine, which is a negligible

Plate 9 Royal blue potato flesh colour



portion of total protein, are of high nutritional quality, Red Pontiac has high-quality protein. Potato tubers had 1.67 % N/dry matter (Gorinstein et al. 1988). Of the total N content, 43 % was dialyzable N and 32.9 % true protein N. The protein, by solubility fractionation, provided 67 % albumin, 23 % globulin, 1.4 % prolamine and 9 % glutelins. Albumin had two major protein species, one of 45×10^3 and the other of $12\text{--}25 \times 10^3$ daltons. Prolamine and glutelins contained protein bands coinciding in molecular weight with those of albumin and globulin. Some minor losses in protein composition of potatoes occurred during processing. Ultrafiltration gave the best yield recovery of protein from potato juice compared to polyelectrolyte coagulation and cryoconcentration (Wojnowska et al. 1981). Depending on the method of potato juice concentration, differences were observed in: foaming and emulsifying properties, wettability, swelling and buffer capacity of preparations. The dried preparations contained a high level of proteolytic enzyme inhibitors and glycoalkaloids. Thermal inactivation of preparations before drying led to 43–48 % destruction of protease inhibitors and 81–89 % glycoalkaloids. At the same time, it was observed that thermal treatment led to distinct changes in the amino acid composition of the proteins and had an adverse effect on the properties of the dried preparations.

Racusen and Foote (1980) reported that a glycoprotein of molecular mass about 45,000 accounted for about 20 % of the total soluble protein in potato and proposed the alternative name

‘patatin’, based on ‘patata’, the original American Indian-derived Spanish word for potato. Park et al. (1983) estimated the molecular mass of patatin to be about 40,000 and showed extensive heterogeneity with forms differing in electrophoretic mobility at pH 8.6 and in mobility on SDS–PAGE. Paiva et al. (1983) demonstrated that there was a linear relationship between the amount of patatin, expressed as a percentage of total soluble protein, and the logarithm of tuber weight from 0.3 to 300 g, with patatin forming about 40 % of the total soluble protein in tubers above about 200 g. Under normal conditions, patatin was found in only trace amounts, if at all, in leaves, stems or roots of plants which were either actively forming tubers or which had been grown under long days to prevent tuberisation. However, if tubers and axillary buds were removed, patatin could accumulate in stems and petioles. Patatin was reported to account for 30–40 % of the total soluble protein in potato tubers (Andrews et al. 1988). Besides being a storage protein, it also exhibited lipid acyl hydrolase and acyltransferase activities. It was active with phospholipids, monoacylglycerols and p-nitrophenyl esters and moderately active with galactolipids but is apparently inactive with di- and triacylglycerols. Isolated patatin at room temperature was found to be a highly structured molecule at both secondary and tertiary levels (Pots et al. 1998). About 33 % of the residues adopted an α -helical and 46 % a β -stranded structure. Patatin was thermally destabilised at temperatures exceeding 28 °C. It was shown that parts of the α -helical

contributions unfold in the 45–55 °C region, whereas the β -stranded parts unfold more gradually at temperatures of 50–90 °C. Patatin from potato tuber was found to have a molecular mass of 45 kDa (Liu et al. 2003). van Koningsveld et al. (2001) reported the soluble potato proteins to mainly compose of patatin and protease inhibitors. Potato proteins were soluble at neutral and strongly acidic pH values. The tertiary structure of patatin was irreversibly altered by precipitation at pH 5. At mildly acidic pH, the overall potato protein solubility was dependent on ionic strength and the presence of unfolded patatin. Thermal unfolding of the protease inhibitors was correlated with a decrease in protease inhibitor activities and resulted in an ionic strength-dependent loss of protein solubility.

Three protein inhibitors of proteolytic enzymes with molecular weights 21, 22 and 23 kD were isolated from potato tubers (Valueva et al. 1997). The 21- and 22-kD proteins were shown to be serine proteinase inhibitors with different specificities. The 21-kD protein inhibited human leucocyte elastase and trypsin effectively but was less effective towards chymotrypsin. The 22-kD protein was an inhibitor of cysteine proteinases and suppressed the activities of papain, ficin and bromelain with the same affinities. None of the isolated proteins inhibited subtilisin, pepsin or cathepsin D. The 21-kD protein consisted of two disulphide-linked polypeptide chains with molecular weights of 16.5 kD and 4.5 kD. The 22-kD and 23-kD proteins possessed a single polypeptide chain. The N-terminal 22–25 amino acid sequences of these three proteins exhibited significant homology to other plant inhibitors from the Kunitz soybean inhibitor superfamily. Three protein proteolytic enzyme inhibitors with molecular masses 21, 22 and 23 kDa were isolated from intact potato tubers (Valueva et al. 1998). The 21 and 22 kDa proteins denoted as PSPI-21 and PSPI-22, respectively, were serine proteinase inhibitors with different specificity. The 23 kDa protein denoted as PCPI-23 was an inhibitor of plant cysteine proteinases. The PSPI-21 molecule consisted of two disulphide-linked polypeptide chains with molecular masses of 16.5 kDa and 4.5 kDa. The

PSPI-22 and PCPI-23 had one polypeptide chain. They exhibited significant homology to other plant inhibitors which were members of the soybean Kunitz inhibitor family. It was found that at least PSPI-21 and PSPI-22 could predominantly accumulate in potato tubers infected with *Phytophthora infestans*. A 21-kD protein isolated earlier from potato tubers was found to have two isoforms, with pI 6.3 and 5.2 (Valueva et al. 1999). The primary structures of the two forms consisted of 187 and 186 amino acid residues. Both isoforms were composed of two polypeptide chains, designated A and B, linked by a single disulphide bond between Cys-146 of the A chain and Cys-7 of the B chain. The amino acid sequences of the A chains of the two forms, consisting of 150 residues each, differed in a single amino acid residue at position 52 (Val \rightarrow Ile), while the B chains, containing 37 and 36 residues, respectively, had substitutions at nine positions (Leu-8 \rightarrow Ser-8, Lys-25--Asp-26 \rightarrow Asn-25-Glu-26, Ile-31--Ser-32 \rightarrow Val-31-Leu-32, Lys-34-Gln-35-Val-36--Gln-37- \rightarrow Gln-34-Glu-35-Val-36). Both isoforms formed stable inhibiting complexes with human leukocyte elastase and were less effective against chymotrypsin and trypsin.

Protein concentrates isolated from potato fruit juice by precipitation with ethanol or ferric chloride afforded exhibited yield of 69 % and 86.5 % of total protein, respectively, and high nutritional value; values of essential amino acid index (EAAI) were 81.7 % and 82.7 %, respectively (Bártová and Bárta 2009). Fraction of patatin proteins (39–43 kDa) represented with EAAI value of 86.1 % the nutritionally improved protein component. Lipid acyl hydrolase activity of patatin family was not negatively affected by cooled ethanol precipitation. Sun et al. (2013) reported that patatin purified from potato fruit juice possessed a monosaccharide composition of rhamnose, mannose, glucose and galactose with a molar ratio of 41:30:21:8, and patatin consisted of (1 \rightarrow 3) linked α -mannose, (1 \rightarrow 4) linked α -galactose, (1 \rightarrow 4) linked β -glucose and (1 \rightarrow 2) linked α -rhamnose. Potato fruit juice, prepared using Canadian variety of potatoes, was found to compose 22.9 % patatin, 53.3 % protease inhibi-

tors and 23.7 % high MW proteins (Waglay et al. 2014). $(\text{NH}_4)_2\text{SO}_4$ precipitation led to the highest yield (98.6 %) and to the recovery of protein isolates enriched in patatin with high resolubility. FeCl_3 precipitation resulted in the highest purification factor (6.2) and isolates with the lowest relative proportion of high MW proteins (<4.6 %). FeCl_3 and MnCl_2 were identified as the best precipitating agents for the enrichment of isolates with >15 kDa protease inhibitors. Trypsin inhibiting activities of protease inhibitors were highly preserved upon protein isolation than the chymotrypsin ones. Acidic-based protein isolate showed the highest specific lipid acyl hydrolase activity of patatin towards o-nitrophenyl butyrate, whereas the FeCl_3 -based one exhibited the highest activity towards 4-nitrophenyl laurate. A protein with molecular weight of 21 kD denoted as PKSI was isolated from potato tubers (*Solanum tuberosum* cv. Istrinskii) (Revina et al. 2004). The N-terminal sequence of the protein consisted of 19 amino acid residues and was highly homologous to sequences of the known inhibitors from group C of the subfamily of potato Kunitz-type proteinase inhibitors. The protein effectively inhibited the activity of subtilisin but was inactive against trypsin, chymotrypsin and the cysteine proteinase papain. A protein of 22 kDa designated as PKTI-22 was isolated from potato tubers (*Solanum tuberosum* cv. Istrinskii) (Revina et al. 2010). The protein efficiently suppressed the activity of trypsin but affected chymotrypsin less and did not affect subtilisin Carlsberg. The N-terminal sequence of PKTI-22 (20 amino acid residues) was found to be highly homologous with the amino acid sequences of the potato Kunitz-type proteinase inhibitors of group B (PKPI-B).

Peřksa et al. (2013) found that the quality of protein depended on potato variety but not on its flesh colour or total protein content. Leucine limited the quality of protein of the majority of coloured potato varieties. Purple-fleshed varieties Vitelotte and Blaue Anneliese, yellow-fleshed Verdi as well as red-fleshed Herbie 26, Highland B. Red and Rosemarie were found to have the best amino acid profiles and essential amino acid index.

Two enzymes involved in the biosynthesis of starch in potato were extracted from potato juice; Q-enzyme in crystalline form was precipitated with ethanol at low temperature (Gilbert and Patrick 1952a) and phosphorylase (Gilbert and Patrick 1952b).

Phytosterols

Free sterols, β -sitosterol and stigmasterol were isolated from white-fleshed potato (Schwartz and Wall 1955). Raw potatoes were found to contain (mg/100 g) 0.98 mg total phytosterols comprising 0.04 mg campesterol, 0.10 mg stigmasterol, 0.54 mg β -sitosterol, 0.30 mg Δ^5 -avensterol and also 0.05 mg squalene (Chiou et al. 2009). In the Katahdin variety of *Solanum tuberosum*, incorporation of mevalonic acid-2- C^{14} into the major sterols, stigmasterol and β -sitosterol, occurred in 1 week (Johnson et al. 1964). Incorporation into β -sitosterol started sooner and occurred to a greater degree than in the case of stigmasterol.

The following phytosterols had been reported to occur in unsaponifiable lipids from potato leaves: β -sitosterol and a methylsterol assumed to be lophenol or citrostadienol (Schreiber et al. 1961); cycloartenol, 24-methyl-cycloartenol and α -sitosterol (Schreiber and Osske 1962, 1963, 1964); lophenol, 24-methylene-lophenol and 4 α -methyl-5 α -stigmastera-7,24(28)-diene-3 β -ol (24-ethylidene-lophenol) (Osske and Schreiber 1965; Schreiber and Osske 1962, 1963, 1964); Δ^5 -campesterol, stigmasterol and cholesterol (Ardenne et al. 1963, 1965; Johnson et al. 1963; Osske and Schreiber 1965) and cyclolaudenol (Schreiber and Osske 1964). From haulm and tuber sprouts of potato cv. Desiree fractions, Δ^5 -sterols and Δ^7 -sterols, 4-methyl-sterols, triterpenic alcohols, tocopherols and hydrocarbons were isolated (Stanković et al. 1990). Sterol and triterpenic alcohol fractions of unsaponifiable lipids of the haulm and tuber sprouts were found to contain twelve sterols and four triterpenic alcohols, respectively. The lipid components identified were cholesterol, campesterol, stigmasterol β -sitosterol, 24*R*-4-stigmasten-3-on, cycloeucalenol, obtusifoliol, lophenol, 24-methylene-lophenol, 24-ethylidene-lophenol, 24-methylene-cycloartanol, cycloartenol, lanosterol, β -amyrin,

phytol, C_{23} -to C_{33-n} -parafins, C_{19} -and C_{31} -cyclohexyl hydrocarbons, C_{22} -to C_{38} -olefins and squalene. 24R-4-stigmasten-3-on, Δ^7 -campesterol, Δ^7 -stigmasterol, lanosterol, cycloeucaleanol and obtusifoliol had not been identified previously in unsaponifiable lipids from haulm and sprouts.

The level of glycoalkaloids present in freshly cut potato tuber discs started to increase after 24 h of incubation (Bergensträhle et al. 1992). This accumulation was inhibited by the sterol synthesis inhibitor, tridemorph, and was thus due to synthesis de novo. Concomitant to the accumulation of glycoalkaloids, there was an increase in the specific activity of a glycoalkaloid-specific enzyme, UDP-glucose:solanidine glucosyltransferase (solanidine-GT). Other sterol-metabolizing enzymes S-adenosyl-L-methionine:cycloartenol methyltransferase (cycloartenol-MT) exhibited different time-course curves. Addition of ethephon or tridemorph inhibited the accumulation of sterols and sterol precursors in potato tuber discs (Bergensträhle et al. 1996). In the 4,4-dimethylsterol fraction and the 4 α -methylsterol fraction, only compounds with a nonalkylated side chain were found. The 4-desmethylsterols synthesised de novo were, in tridemorph-treated discs, pollinastanol and 5 α -cholest-8-en-3 β -ol; in ethephon-treated discs, isofucosterol; and, in control discs, isofucosterol and cholesterol. The cholesterol concentration decreased concurrently with the accumulation of glycoalkaloids. The results showed that cholesterol synthesis was stimulated in potato discs and indicated cholesterol to be a precursor of glycoalkaloids in potato.

Potato Starch

The amylose content of starches ranged between 15.0 % and 23.1 % and differed significantly among different potato cultivars (Kaur et al. 2007). Pasting temperatures of different potato starches ranged from 64.5 to 69.5 °C, the highest for Kufri Sindhuri (Patna) and the lowest for Kufri Bahar (Jalandhar). The transmittance value decreased progressively during refrigerated storage of pastes from different potato starches. The transition temperatures (onset temperature (To);

peak temperature (Tp); conclusion temperature (Tc)), gelatinisation temperature range (R) and enthalpies of gelatinization (DH_{gel}) of the starches from different potato cultivars differed significantly. Potato starch showed the presence of exceptionally large size granules. The granules showed the size between 32.37 and 42.05 μ m. Kufri Lauvkar (Gwalior) starch showed the presence of smaller size granules, and Kufri Chipsona-2 (Modipuram) showed larger granules. Ash content ranged from 0.06 to 0.45 %. Swelling power (SP) ranged from 29.27 to 48.61 % and solubility ranged from 4.17 to 36.98 %. Peak viscosity ranged from 4145 to 6803 cP, hot paste viscosity (HPV) 1950–3204 cP, cold paste viscosity (CPV) 2351–3606 cP, setback viscosity 282–436 cP, breakdown (BD) 1850–4490 cP, pasting temperature (Ptemp) 64.50–69.40 °C and pasting time (PT) 3.60–5.70 min. Ash content which mainly represented the phosphorus content in potato starch was positively correlated to hot paste viscosity, To and Tp, and negatively correlated with SP. Amylose content was positively correlated to HPV and cold paste viscosity. Amylose content was negatively correlated to transmittance measured after storage of 0, 24 and 72 h. Solubility was positively correlated with To and Tp. Solubility was positively correlated with To and Tp. PV showed significant positive correlation with BD and negative correlation with PT. HPV showed significant positive correlation with CPV and negative correlation with transmittance. CPV showed positive correlation to PT, Ptemp, Tp and Tc and negative correlation to transmittance. BD showed highly negative correlation with PT and positive correlation with transmittance. Ptemp showed highly positive correlation with transition temperatures To, Tp and Tc and negative correlation with transmittance. To showed significant positive correlation with Tp and Tc and Tp also showed significant positive correlation with Tc. Mean granule size did not correlate significantly with PV, BD and Ptemp.

Scanning electron microscopy showed potato starch granules to be oval and irregular shaped with average diameter of 15 μ m, and the granule diameter increased after storage (Ezekiel et al.

2010). Pasting temperature of starch separated from potato varied from 64.6 to 67.7 °C before storage, and it varied from 66.9 to 69.4 °C after 90-day storage at different temperatures. Peak viscosity was lower after storage at 8 °C and higher at 16 °C. Hot paste viscosity decreased, while breakdown viscosity and set back viscosity increased after storage, and there was no significant change in cold paste viscosity. A significant decrease in pasting time and increase in pasting temperature was observed after storage. Phosphorus content showed significant positive correlation with peak viscosity ($R^2=0.452$) and breakdown viscosity ($R^2=0.685$) and a negative correlation with amylose content ($R^2=-0.674$). X-ray diffraction analysis of potato starch samples revealed B-type pattern. Scanning electron microscopy (SEM) showed the presence of oval and irregular-shaped potato starch granules with a diameter range of 15–16 µm (Ezekiel et al. 2007). Mean granule size of starch separated from potatoes stored at 12 °C ranged from 18 to 25 µm and irradiation treatment resulted in an increase in the proportion of small size granules. The irradiation of potatoes with 0.5 kGy caused a significant increase in setback and pasting temperature. Pasting temperature of starch was observed to vary with the storage temperature. Starch separated from potatoes stored at higher temperature showed lower pasting temperature and vice versa. The starch from potatoes stored at 8 °C showed higher peak, trough and breakdown viscosity and lower setback. Peak viscosity increased and swelling volume decreased with increase in storage temperature.

Miča (1976) found that during storage of potatoes, changes occurred in starch content, starch granule size, phosphorus, potassium and calcium content in the starch. The potassium content decreased during storage as a function of temperature. The phosphorus content decreased at +2 °C and increased at +10 °C. The calcium content increased in the final stage of storage. The phosphorus content in the starch decreased during storage. Onset and peak transition temperatures and gelatinisation enthalpy of potato starch from 42 potato genotypes intercorrelated (Kim et al. 1995). Transition temperatures intercorre-

lated with pasting temperature. Gelatinisation enthalpy correlated with Brabender pasting temperature and peak paste viscosity, and onset temperature correlated with phosphorus content. Potato starch differential scanning calorimetry (DSC) characteristics did not correlate with amylose, intrinsic viscosity or water binding.

The physico-chemical properties of Irish potato starch were reported by Nwokocha et al. (2014) as follows: 14.64 % moisture, 0.11 % ash, 0.23 % fat, 0.07 % nitrogen, 0.07 % phosphorus and 25.08 % amylose; particle characteristics (particle number 97, maximum diameter 47 mm, minimum diameter 13.39 mm, mean diameter 28.58 mm, length/diameter 1.37, roundness 0.68); gelatinisation properties (onset temperature 61.3 °C, peak temperature 64.2 °C, completion temperature 67 °C, gelatinisation range 5.7 °C, endothermic enthalpy 14.35 J/g); and pasting properties (pasting temperature 69 °C, temperature at peak viscosity 95 °C, peak viscosity during heating (PV) 750 BU, viscosity at 95 °C 750 BU, viscosity after 30 min holding at 95 °C (HPV) 475 BU, viscosity on cooling to 50 °C (CPV) 800 BU, stability ratio (HPV/PV) 0.63, setback ratio (CPV/HPV) 1.89). Irish potato had a paste clarity of 6.5 and syneresis of 3.55 % based on 1 % and syneresis on 5 % aqueous starch pastes. Irish potato had larger starch granules, higher phosphorus and lower amylose contents than sweet potato starch. It also exhibited a lower gelatinisation temperature, higher swelling power and amylose leaching compared to sweet potato starch. Sweet potato starch exhibited a higher pasting temperature, higher paste stability and setback ratio and greater stability to shear thinning than Irish potato starch. The rheological properties indicated non-Newtonian behaviour for the two starch pastes. The storage and loss moduli of the two starch pastes were frequency dependent with values higher for sweet potato at all points within the angular frequency range employed. Irish potato starch paste exhibited higher paste clarity and lower syneresis than sweet potato starch paste. Irish potato has superior properties for application as thickener, while sweet potato is better in withstanding severe processing conditions. The extent of the annealing

effect of potato starch depended on the difference between onset and annealing temperatures, and prolonged treatment time increased the effect (Karlsson and Eliasson 2003). Treating samples at 50 °C for 24 h caused a shift in gelatinisation onset temperature of 11–12 °C for isolated starch and 7–11 °C for in situ samples. Starch/water systems and tissue samples behaved similarly when exposed to time/temperature treatments. The starches separated from mealier potato cultivars (Kufri Jyoti and Kufri Badshah) showed lower transition temperatures (T_0 ; T_p and T_c) and peak height indices (PHI) and higher gelatinisation temperature range (R) and enthalpies of gelatinisation (ΔH_{gel}) than the starch from least mealy cultivar (Pukhraj) (Kaur et al. 2002). Swelling power, solubility, amylose content and transmittance values were observed to be higher for Kufri Jyoti and Kufri Badshah potato starches, while turbidity values were lower for these starches. The rheological properties of starches showed significant variation in the peak G' , G'' and peak $\tan \delta$ values. Kufri Badshah and Kufri Jyoti starches showed higher peak G' , G'' and lower peak $\tan \delta$ values than Pukhraj starch during heating and cooling cycles. Kufri Jyoti and Kufri Badshah starches showed higher breakdown in G' than starch from the Pukhraj potato cultivar. The large-sized granules of the starches from Kufri Badshah and Kufri Jyoti appeared to be associated with higher values of peak G' and G'' and consistency coefficient. Starch from the least mealy cultivar (Pukhraj) showed higher retrogradation, which increased progressively during storage at 4 °C for 120 h.

In all potato starches examined, the phosphorus content ranged from 308 to 1244 ppm (Noda et al. 2007). Furthermore, samples differing manifestly in their phosphorus content indicated that enhancing the starch phosphate resulted in significant increases in the swelling power, peak viscosity and breakdown and significant but small increases in the onset and peak temperatures of gelatinisation. Other starch quality parameters, such as the amylose content, median granule size and the gelatinisation enthalpy, did not change significantly due to the degree of phosphate substitution of starch. The amylose of potato starches

had a negative correlation with the peak viscosity (PV) and breakdown (BD) and a positive correlation with the setback viscosity (SV) and peak viscosity temperature (PVT) (Zaidul et al. 2007). By contrast, phosphorus had a positive correlation with PV, BD and SV and a negative correlation with PVT. In addition, the median granule size had a positive correlation with PV and BD. By contrast, a negative correlation of the median granule size was observed with SV and PVT. The correlation coefficients of amylose–phosphorus, amylose–granule size and phosphorus–granule size interactions indicated that amylose had more influence than had phosphorus or had the median granule size on PV and BD.

Starch and K content of potato tubers increased with progressing age, whereas a decrease was observed in growth rate, starch synthesis per day and K uptake per day (Lindhauer and De Fekete 1990). Positive correlations between the rates of K uptake, starch production and growth indicate that the dynamic phase of K supply to the tubers was of greater importance for starch synthesizing processes than the influence of total K content. The activity of starch synthesis enzymes (sucrose synthase, UDP-D-glucose pyrophosphatase, starch phosphorylase, amylases) related to tuber K content did not differ significantly. Of the purified potato starch branching enzyme (SBE) I and SBE II, the former was more active than SBE II on an amylose substrate, whereas SBE II was more active than SBE I on an amylopectin substrate (Rydber et al. 2001). Both enzymes were stimulated by the presence of phosphate. After debranching of the products, the majority of dextrans with a degree of polymerisation (dp) greater than 60 were absent for SBE I and those with a dp greater than 70 for SBE II. Full-length cDNAs encoding a second starch branching enzyme (SBE A) isoform was isolated from potato tubers (Jobling et al. 1999). The predicted protein has a molecular mass of 101 kDa including a transit peptide of 48 amino acids. Multiple forms of the SBE A gene exist which differ mainly in the length of a polyglutamic acid repeat at the C-terminus of the protein. High-amylose starch is in great demand by the starch industry for food and industrial applications for its unique func-

tional properties. A very high-amylose potato starch was produced by genetic modification through simultaneously inhibiting two isoforms of starch branching enzyme to below 1 % of the wild-type activities (Schwall et al. 2000). The amylose content was increased to levels comparable to the highest commercially available maize starches. Additionally, the phosphorus content of the starch was increased more than fivefold. The granular interior of octenylsuccinic maize starch had higher fluorescent intensity than that of octenylsuccinic potato starch (Wang et al. 2013). The degree of substitution of octenylsuccinic maize starch degraded less than that of octenylsuccinic potato starch under the same degree of gelatinisation. The results implied that maize starch displayed much more homogeneous octenylsuccinic anhydride reaction pattern when compared to potato starch.

Carotenoids

The carotenoid pattern in four yellow- and four white-fleshed potato cultivars (*S. tuberosum*) was dominated by violaxanthin, antheraxanthin, lutein and zeaxanthin, which were present in different ratios, whereas neoxanthin, β -cryptoxanthin and β , β -carotene generally were only minor constituents (Breithaupt and Bamedi 2002). Antheraxanthin was found to be the only carotenoid epoxide present in native extracts. The total concentration of the four main carotenoids reached 175 $\mu\text{g}/100\text{ g}$, whereas the sum of carotenoid esters accounted for 41–131 $\mu\text{g}/100\text{ g}$. Therefore, carotenoid esters were regarded as quantitatively significant compounds in potatoes. Carotenoid contents reported in potatoes ranged from 50 to 100 μg per 100 g fresh weight (FW) in white-fleshed varieties to 2000 μg per 100 g FW in deeply yellow to orange-fleshed cultivars (Brown 2005). The carotenoids in potato were mainly xanthophylls: lutein, zeaxanthin and violaxanthin with traces of either α -carotene or β -carotene, indicating potato to be not a source of provitamin A carotenes. White- and yellow-fleshed potato contained xanthophyllous carotenoids (Brown 2006). The total carotenoid content of white cultivars and breeding lines ranged from 50 to 100 μg per 100 g FW. Yellow-

fleshed cultivars may have carotenoid contents up to 270 μg , while more intensely yellow breeding clones will range up to 800 μg . Although the concentration of anthocyanin in skin tissue was quite high, it constituted such a small volume of the whole tuber that generally a red-skinned white-fleshed potato had no more than 1.5 mg per 100 g FW when skin and flesh were extracted together. However, potatoes with anthocyanin in the flesh ranged from 15 to nearly 40 mg per 100 g FW. Carotenoids are found in all potatoes in the flesh (Brown et al. 2008). White-fleshed varieties were reported to contain 50 to 100 μg per 100 g fresh weight (FW) and moderately yellow-fleshed varieties 100 to 350 μg per 100 g FW. The more intensely yellow-fleshed genotypes, which may look orange, at the higher extremes contained levels above 1000 μg per 100 g FW. The highest level published is 2600 μg per 100 g FW in diploid germplasm derived from South American *Papa Amarilla* cultivars. Potato generally possessed predominantly lutein, a xanthophyll, also found in the human retina, and must be obtained in the diet. The genotypes with extremely high levels of total carotenoids had zeaxanthin, an isomer of lutein, also present in the human retina. Total anthocyanins ranged from 1.5 mg to 48 mg per 100 g FW in a solidly pigmented purple-skinned, purple-fleshed breeding line.

Based on the carotenoid profile, sixty potato cultivars (commercial, bred, old and native cultivars) were segregated into three groups according to the major pigment in the carotenoid profile: violaxanthin (37 cultivars, especially those with higher carotenoid content), lutein (16 cultivars) and neoxanthin (7 cultivars) (Fernandez-Orozco et al. 2013). Other minor carotenoids were antheraxanthin, β -cryptoxanthin and β -carotene, while zeaxanthin was absent in all sample. The total carotenoid content ranged from 50.0 to 1552.0 $\mu\text{g}/100\text{ g}$ dry wt, with an average value of about 435.3 $\mu\text{g}/100\text{ g}$ dry wt. Sipancachi, Poluya and Chaucha native cultivars showed the highest carotenoid content (1020.0, 1478.2 and 1551.2 $\mu\text{g}/100\text{ g}$ dry wt, respectively). Xanthophyll esters were present in most cultivars, mainly as diesterified forms, being observed

a direct correlation between the carotenoid content and the esterified fraction, suggesting that the esterification process facilitated the accumulation of these lipophilic compounds within the plastids. Yellow-fleshed potatoes were found to contain significant amounts of lutein and zeaxanthin (Burgos et al. 2013). The gastric and duodenal digestive stability of lutein and zeaxanthin in boiled tubers of the different accessions ranged from 70 to 95 %, while the efficiency of micellarisation ranged from 33 to 71 % for lutein and from 51 to 71 % for zeaxanthin. For all accessions, amounts of lutein and zeaxanthin after micellarisation were significantly lower than the original amount found in the boiled samples. The accession 701862 showed the highest bioaccessible lutein concentration (280 µg/100 g, FW), and the accessions 703566 and 704218 showed the highest bioaccessible zeaxanthin concentration (above 600 µg/100 g, FW). Considering the mean potato intake in the Andes (500 g per day), the accession 701862 provides 14 % of the lutein intake suggested for health benefits, and the accessions 703566 and 704218 provide 50 % more than the suggested zeaxanthin intake.

Phenolic Compounds (Phenolic Acids, Flavonoids and Anthocyanins)

Phenolic compounds could be broadly classified into phenolic acids (C6-C1 and C6-C3 structures) and flavonoids (C6-C3-C6 backbone) (Schieber and Saldaña 2009). They reported the following phenolic compounds in potatoes: (a) hydroxycinnamic acids, 5-*O*-caffeoylquinic acid (chlorogenic acid), 4-*O*-caffeoylquinic acid (cryptochlorogenic acid), 3-*O*-caffeoylquinic acid (neochlorogenic acid) and *p*-coumaric acid and ferulic acid; (b) hydroxybenzoic acids, gallic acid, protocatechuic acid, vanillic acid and salicylic acid; (c) non-anthocyanin flavonoids, catechin, epicatechin, eriodictiol, naringenin, kaempferol glycosides and quercetin glycosides; (d) anthocyanins, petunidin glycosides, malvidin glycosides, pelargonidin glycosides and peonidin glycosides; and (e) dihydrocaffeoyl polyamines, *N*¹,*N*¹²-bis(dihydrocaffeoyl)spermine (kukoamine A); *N*¹,*N*⁸-bis(dihydrocaffeoyl)spermidine; *N*¹,*N*⁴,*N*¹²-tris(dihydrocaffeoyl)spermine and *N*¹,*N*⁴,

*N*⁸-tris(dihydrocaffeoyl)spermidine. Besides chlorogenic acid and its isomers, caffeic, *p*-coumaric and ferulic acids as well as various benzoic acid derivatives such as gallic, protocatechuic, vanillic and salicylic acids were found in potato peels, however, usually in lower amounts (Onyeneho and Hettiarachchy 1993; De Sotillo et al. 1994a; Lewis et al. 1998a; Mattila and Hellström 2007). About 50 % of the phenolic compounds were found to be located in the potato peel and adjoining tissues, while the rest decreased in concentration from the outside towards the centre of potato tubers (Hasegawa et al. 1966). Freeze-dried aqueous extracts of potato peel waste were found to contain chlorogenic (50.31 %), gallic (41.67 %), protocatechuic (7.81 %) and caffeic (0.21 %) acids as major phenolics (De Sotillo et al. 1994b). The greatest amounts of phenolic acids resulted when potato peel waste homogenate was refluxed with water for 30 min yielding a total concentration of 48 mg/100 g (De Sotillo et al. 1994a). Four phenolic acids (chlorogenic, gallic, protocatechuic and caffeic) were characterised as major components. Aqueous extracts were stored 20 days and after 7 days at 25 °C exposed to light; chlorogenic acid had degraded to caffeic acid. Nara et al. (2006) found that in potato peels phenolic acids were not only present in their free form but occurred also in bound form, as shown for ferulic acid. The total polyphenolic content in potato peel was found to be 3.93 mg/g powder, and the major phenolic acids present were predominantly gallic acid, caffeic acid, chlorogenic acid and protocatechuic acid (Singh and Rajini 2008). The total phenolic acid content of potato flowers (626 mg/100 g fresh wt) was 21 and 59 times greater than that of leaves and stems, respectively (Im et al. 2008). For all samples, chlorogenic acid and its isomer contributed 96–98 % to the total. Total phenolic acid levels (in g/100 g fresh wt) of peels of five potato varieties grown in Korea ranged from 6.5 to 42.1 and of the flesh (pulp) from 0.5 to 16.5, with peel/pulp ratios ranging from 2.6 to 21.1. The total phenolic acid content for 25 American potatoes ranged from 1.0 to 172. The highest amounts were present in red and purple potatoes. Home processing of pulp with vari-

ous forms of heat induced reductions in the phenolic content. Eleven compounds were isolated from potato peels and included chlorogenic acid, other phenolic compounds, 2 glycoalkaloids, 3 low molecular weight amide compounds and 2 unsaturated fatty acids, including an ω -3 fatty acid (Wu et al. 2012). The potato peels contained a higher amount of phenolic compounds than the flesh. Among the different solvents tested, methanol exhibited the highest extraction ability for phenolic compounds from potato peels, with total phenolics amounting to 2.91 mg gallic acid equivalent/g dry weight (Mohdaly et al. 2010, 2013). The phenolic acid compounds found in the potato peels included: chlorogenic, caffeic, gallic, ferulic, *p*-hydroxybenzoic, *p*-coumaric and *trans*-*O*-hydroxycinnamic acids. Deusser et al. (2012) reported that chlorogenic acid and its isomers, neochlorogenic and cryptochlorogenic acids, were the major phenolic compounds in potato peel. Glycoalkaloid contents were highest in the peel and lowest in the inner flesh. Potato peel as a source of dietary fibre in bread was found to be superior to wheat bran in the contents of certain minerals, in total dietary fibre, in water-holding capacity, in its lower quantity of starchy components and in its lack of phytate (Toma et al. 1979). These dietary advantages were not lost in baking quality trials.

Four related phenolic amides were detected during metabolic profiling of potato (*Solanum tuberosum*) tubers (Parr et al. 2005). They were identified as N^1, N^{12} -bis(dihydrocaffeoyl)spermine (kukoamine A); N^1, N^8 -bis(dihydrocaffeoyl)spermidine; N^1, N^4, N^{12} -tris(dihydrocaffeoyl)spermine; and N^1, N^4, N^8 -tris(dihydrocaffeoyl)spermidine. Solid phase extraction (SPE) of N^1, N^{12} -bis(dihydrocaffeoyl)spermine (kukoamine A) from potato peels was optimised using a molecularly imprinted polymer (MIP) (Piletska et al. 2012). The kukoamine A purified from potato extract using MIP was exceptionally pure ($\approx 90\%$). Kukoamines (kukoamin A) had been associated with reduced blood pressure (Funayama et al. 1980), and they had also been used to treat trypanosomiasis, a type of sleeping sickness caused by parasitic trypanosomatids like *Crithidia fasciculata* (Ponasik et al. 1995).

Kukoamine A inhibited trypanothione reductase as a mixed inhibitor ($K_i = 1.8\ \mu\text{M}$, $K_{ii} = 13\ \mu\text{M}$). Kukoamine shows no significant inhibition of human glutathione reductase ($K_i > 10\ \text{mM}$) and thus provided a novel selective drug lead.

The free phenolic compounds found in four potato cultivars in Tenerife (Canary Islands) were (+)-catechin, chlorogenic acid, caffeic acid, *p*-coumaric acid and ferulic acid (Verde Méndez et al. 2004). A significant and negative correlation was established between (+)-catechin and *p*-coumaric acid. A considerable contribution to the daily intake of flavonoids was observed with the actual consumption of potatoes. Range of phenolic compounds (mg/100 g dm) in tubers of varying flesh colour was reported by Navarre et al. (2011) as follows: yellow type, 1.1–20.1 mg neochlorogenic acid, 0.7–4.5 mg caffeoyl putrescine, 22.9–211 mg chlorogenic acid, 3.8–32.7 mg cryptochlorogenic acid, 0.5–9.6 mg caffeic acid, 1.36–14.1 mg rutinose and 0.31–4.49 mg kaempferol-3-rutinose; white type, 0.7–10.7 mg neochlorogenic acid, 0.6–12 mg caffeoyl putrescine, 31–170 mg chlorogenic acid, 3.8–22.8 mg cryptochlorogenic acid, 4.7–14.4 mg caffeic acid, 0.37–6.91 mg rutinose and 0.13–1.37 mg kaempferol-3-rutinose; white/purple type, 0.1–18.8 mg neochlorogenic acid, 0.2–16 mg caffeoyl putrescine, 21.9–231 mg chlorogenic acid, 1.0–22.47 mg cryptochlorogenic acid, 2.0–47.6 mg caffeic acid, 0.29–1.72 mg rutinose and 0.15–2.5 mg kaempferol-3-rutinose; red/purple type, 2.9–43.7 mg neochlorogenic acid, 1.3–8.7 mg caffeoyl putrescine, 80.4–473 mg chlorogenic acid, 12.6–63.9 mg cryptochlorogenic acid, 5.2–15.9 mg caffeic acid, 0.48–3.54 mg rutinose, and 0.46–0.3 mg kaempferol-3-rutinose. Chlorogenic acids (CGA) concentrations in potato skins were 37–636 mg/100 g dry weight (DW) and were three to four times greater than those in the flesh (Weidel et al. 2014). Storage reduced the CGA levels in potatoes by up to 81%. The studied potato purees contained 4–11 mg CGA/100 g DW. In addition, the quinic acid contents of potato flesh (11–95 mg/100 g DW) and puree (11–22 mg/100 g DW) were determined. None of the tested samples contained caffeic acid.

Coloured-fleshed potato varieties were characterised by about three times higher amount of total phenolic content than traditional yellow-fleshed ones (Rytel et al. 2014). The predominating phenolic acids in potato were chlorogenic acid and its isomers, which account about 90 % of total phenolic content in tubers. The phenolic acid content decreased by 80 % after peeling the blue-fleshed potatoes and by 60 % after peeling the yellow variety. The dried potato dice obtained from yellow-fleshed potatoes had no content of phenolic acids, but those produced from coloured-fleshed potatoes contained about 4 % of the original phenolic content of the raw material. Chlorogenic acid amounted about 97 % of total phenolic acid content, and the rest was neochlorogenic acid. Concentrations of total phenolics in yellow (3.2 g/kg) and purple (3.1 g/kg) potato cultivars were twofold greater than in the white potato cultivar (1.5 g/kg) (Kaspar et al. 2013). Anthocyanins were low to non-detectable in white (0 g/kg) and yellow potatoes (0.3 g/kg). Purple potatoes anthocyanin concentration (6.2 g/kg) was 20-fold greater than in yellow potatoes (0.3 g/kg) and white potatoes (0 g/kg). Carotenoid concentrations in white and purple potatoes were similar (1.3 mg/kg), while yellow potatoes had a 45-fold greater carotenoid concentration (58.1 mg/kg) compared to white and purple potatoes. Consumers ranked the aroma and appearance of white and yellow potatoes higher than purple potatoes. However, no significant differences were observed in overall acceptance between the potato cultivars. Four individual anthocyanins were detected as the major components of a purple potato cultivar, and the total anthocyanin content was 273.5 mg of cyanidin-3-glucoside equiv/100 g of dry seeds (Zhao et al. 2011). Purple potato anthocyanins delayed the quenching of bovine serum albumin (BSA) caused by chromium. It was found that the anthocyanin could protect the secondary and tertiary structures of BSA by probably interacting with chromium in advance.

Over 30 compounds were identified in potato tubers: ascorbic acid, tyrosine, phenylalanine and tryptophan; quinic acid derivative; caffeic acid; 1-*O*-caffeoyl quinic acid; 5-*O*-feruloyl quinic acid;

4,5-di-*O*-caffeoyl quinic acid; caffeoyl- β -glucose; caffeic acid derivative; chlorogenic acid; neochlorogenic acid; cryptochlorogenic acid; 3-*O*-caffeoyl,5-*O*-feruloylquinic acid; quercetin-3-*O*-glu-rut; caffeoyl methyl quinate; gentisic acid glucoside; salicylic acid glucoside; ferulic acid amide; rutin; quercetin; quercetin dimethyl ether; kaempferol-3-*O*-glucoside; caffeoyl putrescine; caffeoyl spermine derivative; bis(dihydrocaffeoyl)spermine; bis(dihydrocaffeoyl)spermidine; tri(dihydrocaffeoyl)spermine; N^1, N^4, N^8, N^{12} -tetra(dihydrocaffeoyl)spermine; N^1, N^4, N^8 -tris(dihydrocaffeoyl)spermidine; solanine; and chaconine (Shakya and Navarre 2006). Some of these were deemed to possess either nutritional value in functional foods or were involved in plant disease resistance

Pigmented potato (*Solanum tuberosum*) varieties were found to be a rich source of anthocyanins, a subgroup of flavonoids, in particular acylated derivatives (Eichhorn and Winterhalter 2005). Petunidin derivatives were detected in all varieties except Highland Burgundy Red, where pelargonidin was found to be the only anthocyanidin. Malvidin was the predominant aglycone of the variety Vitelotte. Of the four selected cultivars, Shetland Black was the only one containing minor amounts of peonidin derivatives. Coumaric acid derivatives (i.e. 3-*p*-coumaroylrutinoside-5-glucosides of petunidin, pelargonidin, peonidin and malvidin) were separated from non-acylated anthocyanins as well as chlorogenic acids by means of solid phase extraction, countercurrent chromatography and preparative HPLC.

The flavonoids, in order of abundance, were reported to be catechin, epicatechin, eriodictyol, kaempferol and naringenin (Brown 2005). Potatoes were reported to contain phenolic compounds, with chlorogenic acid predominating and constituting about 80 % of the total phenolic acids. Up to 30 μ g per 100 g FW of flavonoids was present in the flesh of white-fleshed potatoes with roughly twice the amount present in red- and purple-fleshed potatoes. The predominant flavonoids were catechin and epicatechin. Red and purple potatoes derived their colour from anthocyanins. The skin alone may be pigmented, or the flesh may be partially or entirely pig-

mented. Whole unpeeled with complete pigmentation in the flesh may have up to 40 mg per 100 g FW of total anthocyanins. Red-fleshed potatoes possessed acylated glucosides of pelargonidin, while purple potatoes had, in addition, acylated glucosides of malvidin, petunidin, peonidin and delphinidin.

Verma et al. (1972) found that light-grown and dark-grown potato sprouts of cv. Kufri Sindhuri and Kufri Sheetman contained anthocyanins, pelargonidin 3-rhamnoglucoside 5-glucoside and acylated pelargonidin, while light-grown sprouts of Kufri Chamatkar and Kufri Sheetman contained pelargonidin glucoside. Dark-grown sprouts of Kufri Chamatkar contained leucocyanidin(s), while pigmentation was visually observed in the light-grown sprouts of the same variety. Lewis et al. (1998a) identified and quantified the major anthocyanins, flavonoids and phenolic acids in the tubers (skin and flesh), flowers and leaves of 26 cultivars of *Solanum tuberosum* with coloured skins and/or flesh. Red tubers contained mostly pelargonidin-3-(*p*-coumaroyl-rutinoside)-5-glucoside (200–2000 µg/g FW) plus lesser amounts of peonidin-3-(*p*-coumaroyl-rutinoside)-5-glucoside (20–400 µg/g FW). Light to medium purple tubers contained petunidin-3-(*p*-coumaroyl-rutinoside)-5-glucoside (1000–2000 µg/g FW) plus small amounts of malvidin-3-(*p*-coumaroyl-rutinoside)-5-glucoside (20–200 µg/g FW), while dark purple to black tubers contained similar levels of petunidin-3-(*p*-coumaroyl-rutinoside)-5-glucoside together with much higher concentrations of malvidin-3-(*p*-coumaroyl-rutinoside)-5-glucoside (2000–5000 µg/g FW). Tuber flesh also contained chlorogenic acid (30–900 µg/g FW) and lower amounts of vanillic, caffeic, sinapic, gallic, syringic, *p*-coumaric and cinnamic acids plus low concentrations of flavonoids (0–30 µg/g FW). Tuber skins showed much higher levels (1000–4000 µg/g FW) of chlorogenic acid. The major anthocyanins in flowers were present as the rutinosides or other glycosides of pelargonidin, petunidin and malvidin, while glycosides of cyanidin and delphinidin were found in some flowers, together with many

of the same phenolic acids as found in tubers. The commonest flavonoids included rutin, kaempferol-3-rutinoside and two quercetin-rhamnose glucosides. Flowers and leaves contained higher concentrations of flavonoids which fell into two patterns, with some cultivars containing high concentrations of quercetin-3-glycosides, while others had much lower concentrations. Principal component analysis (PCA) revealed a strong association between the various coloured *S. tuberosum* cultivars with distinct differences from the other wild *Solanum* species (Lewis et al. 1998b). Similarly, PCA showed that there were close correlations between the tuber skin and flesh components. The major flavonoids in the skin and flesh were catechin, epicatechin, eriodictyol and naringin. Two acylated pelargonidin glycosides were isolated from red tubers of an anthocyanin-rich tetraploid potato (hybrid seedlings between cultivars of *Solanum tuberosum* and *S. andigena*) (Naito et al. 1998). In cultivars with less coloured potato tubers, the developing tubers remained white for a longer time, with anthocyanin concentrations increasing gradually up to a maximum at a certain tuber weight depending on the cultivar (Lewis et al. 1999). The concentration of flavonoids was lower than that of anthocyanins but followed a similar pattern. Phenolic acid levels were about twice those of the anthocyanins and reached their maximum at a slightly lower tuber weight than anthocyanins and flavonoids. During cold storage (4 °C), the anthocyanin concentration in coloured tubers increased, whereas tubers stored at higher temperatures did not show this increase. The distribution of anthocyanins altered during tuber development and also during cold storage. The major pigment was identified as pelargonidin 3-*O*-(4"-*O*-(*trans-p*-coumaroyl)-α-L-6"-rhamnopyranosyl-β-D-glucopyranoside]-5-*O*-[β-D-glucopyranoside) and the minor pigment as pelargonidin 3-*O*-(4"-*O*-(*trans*-ferruloyl)-α-L-6"-rhamnopyranosyl-β-D-glucopyranoside)-*O*-[β-D-glucopyranoside]. Also detected were pelargonidin-3-acylrutinoside-5-glucoside, *p*-coumaric and ferulic acids. The main anthocyanins (acylated with caffeic acid) of purple sprouts of a Norwegian potato cultivar, *Solanum*

tuberosum isolated from a purified methanolic extract, were determined to be the novel anthocyanins, petunidin 3-*O*-[6-*O*-(4-*O*-*E*-caffeoyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside (10 %) and peonidin 3-*O*-[6-*O*-(4-*O*-*E*-caffeoyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside (6 %) in addition to petunidin, 3-*O*-[6-*O*-(4-*O*-*E*-*p*-coumaroyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside, petanin (37 %), and peonidin 3-*O*-[6-*O*-(4-*O*-*E*-*p*-coumaroyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside, peonanin (25 %) (Fossen et al. 2003). The same major anthocyanins, however, in other proportions (4, 54, and 32 %, for 1, 3 and 4, respectively), were also found in the thin violet zone located in the flesh 0.5–1 cm from the surface of the tubers. On average the highest amounts of anthocyanins were found in the skin (0.65 g/kg FW) of 27 potato cultivars and four breeding clones (Jansen and Flamme 2006). The corresponding values of samples taken from whole tubers (0.31 g/kg FW) and flesh (0.22 g/kg FW) were significantly lower. Among them Peru Purple revealed the highest anthocyanin content in the skin with 2.96 g/kg FW. A similar high value was reached by Violettfleischige and clone 1.81.202–92 N. There were considerable differences in the amounts of anthocyanins between the 31 cultivars/breeding clones. There were also no significant changes in the anthocyanin contents of tubers during storage for 135 days. In dry matter, starch and protein contents, the coloured potato cultivars/breeding clones were comparable with traditional cultivars. Glycoalkaloids were mainly localised in the skin of coloured potatoes. The major anthocyanin glycosides found in purple and coloured potato tubers were pelargonidin 3-[6-*O*-(4-*O*-*E*-*p*-coumaroyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside; peonidin 3-[6-*O*-(4-*O*-*E*-*p*-coumaroyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside; petunidin 3-[6-*O*-(4-*O*-*E*-*p*-coumaroyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside; peonidin 3-[6-*O*-(4-*O*-*E*-caffeoyl-*O*- α -rhamnopyranosyl)- β -D-

glucopyranoside]-5-*O*- β -D-glucopyranoside; petunidin 3-[6-*O*-(4-*O*-*E*-caffeoyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside; petunidin 3-[6-*O*-(4-*O*-*E*-feruoyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside; malvidin 3-[6-*O*-(4-*O*-*E*-feruoyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside; and malvidin 3-[6-*O*-(4-*O*-*E*-*p*-coumaroyl-*O*- α -rhamnopyranosyl)- β -D-glucopyranoside]-5-*O*- β -D-glucopyranoside (Lachman and Hamouz 2005).

In an antioxidant profiling study of 23 Andean potato cultivars, concentrations of the health-promoting carotenoids, lutein and zeaxanthin, ranged from 1.12 to 17.69 μ g/g of dry weight (DW) and from 0 to 17.7 μ g/g of DW, with cultivars 704353 and 702472 showing the highest levels in lutein and zeaxanthin, respectively (Andre et al. 2007b). In contrast, β -carotene was rarely reported in potato tubers; remarkable levels of this dietary provitamin A carotenoid were detected in 16 native varieties, ranging from 0.42 to 2.19 μ g/g of DW. The amount of α -tocopherol found ranged from 2.73 to 20.80 μ g/g of DW and was clearly above the quantities generally reported for commercial varieties. Chlorogenic acid and its isomers dominated the polyphenolic profile of each cultivar. Dark purple-fleshed tubers from the cultivar 704429 contained exceptionally high levels of total anthocyanins (16.33 mg/g of DW). The main anthocyanin was identified as petanin (petunidin-3-*p*-coumaroylrutinoside-5-glucoside). Pigmented potato varieties are a rich source of anthocyanins, in particular acylated derivatives. The major anthocyanins found in pigmented potatoes (e.g. purple-fleshed varieties) include coumaric acid derivatives (i.e. 3-*p*-coumaroylrutinoside-5-glucosides of petunidin, pelargonidin, peonidin and malvidin) from non-acylated anthocyanins as well as chlorogenic acids. Dark purple-fleshed potato contained exceptionally high levels of total anthocyanins, and the main anthocyanin was identified as petanin.

The free phenolic compounds found in Tenerife (Canary Islands) potato samples were (+)-catechin, chlorogenic acid, caffeic acid,

p-coumaric acid and ferulic acid (Del Mar Verde Méndez et al. 2004). Potato samples belonging to Colorado cultivar, ssp. *andigena*, had mean concentrations of total phenolic compounds and chlorogenic acid higher than those found for Kerr's Pink and Cara cultivars, ssp. *tuberosum*, and for Negra cultivar, *S. x chaucha*. In contrast, *p*-coumaric acid was not detected in any potato samples of the Colorado cultivar. Traditional potatoes presented a higher mean concentration of ferulic acid than recently imported potatoes. Polyphenol (phenolic acids, flavanols and flavonols) contents decreased from the tuber peel (2 mm) via the outer (1 cm) to the inner flesh and differed among potato cultivars grown in Luxembourg (Deusser et al. 2012). The cultivars Vitelotte and Luminella had the highest polyphenol contents (5202 and 572 µg/g dry weight (DW) in the outer flesh), whereas Charlotte and Bintje had the lowest contents (19.5 and 48.0 µg/g DW). Chlorogenic acid and its isomers (neo- and cryptochlorogenic acid) were the major polyphenols. Glycoalkaloid (α -chaconine and α -solanine) contents were highest in the peel and lowest in the inner flesh; values in the flesh were below guideline limits in all cultivars. Phenylpropanoids, including chlorogenic acid (CGA), were higher in potato samples from the northern latitudes, as was the expression of phenylpropanoid genes including phenylalanine ammonia lyase (PAL), which had over a tenfold difference in relative abundance (Payyavula et al. 2012). Phenylpropanoid gene expression appeared coordinately regulated and was well correlated with metabolite pools, except for hydroxycinnamoyl-CoA:quinatehydroxycinnamoyl transferase. Anthocyanins were more abundant in Alaskan samples and correlated with flavonoid genes including dihydroflavonol-4-reductase (DFR) ($R^2=0.91$), UDP-glucose:flavonoid 3-*O*-glucosyltransferase (UFGT) ($R^2=0.94$) and flavanone 3-hydroxylase (F3H) ($R^2=0.77$). The most abundant anthocyanin was petunidin-3-coum-rutinoside-5-glucoside, which ranged from 4.7 mg/g in Alaska to 2.3 mg/g in Texas. Positive correlations between tuber sucrose and anthocyanins ($R^2=0.85$) suggested a stimulatory effect of sucrose. Smaller variation was observed in total

carotenoids, but marked differences occurred in individual carotenoids, which had over a tenfold range. Violaxanthin, lutein and zeaxanthin were the predominant carotenoids in tubers from Alaska, Texas and Florida, respectively. Unlike in the phenylpropanoid pathway, poor correlations occurred between carotenoid transcripts and metabolites. Among purple, white and yellow potatoes, purple potatoes contained the most total phenolics, which decreased during development (from 14 to 10 mg/g), as did the activity of phenylalanine ammonia lyase (Payyavula et al. 2013). The major phenolic, 5-chlorogenic acid (5CGA), decreased during development in all cultivars. Products of later branches of the phenylpropanoid pathway also decreased, including quercetin 3-*O*-rutinoside, kaempferol 3-*O*-rutinoside and petunidin 3-*O*-(*p*-coumaroyl) rutinoside-3-glucoside (from 6.4 to 4.0 mg/g). Violaxanthin and lutein were the two most abundant carotenoids and decreased 30–70 % in the yellow and white potatoes. Sucrose, which could regulate phenylpropanoid metabolism, decreased with development in all cultivars and was highest in purple potatoes. Total protein decreased by 15–30 % in two cultivars. Expression of most phenylpropanoid and carotenoid structural genes decreased during development. Navarre et al. (2013) found that the nutritional value of potatoes varied in accordance with changes in phenylpropanoid metabolism during tuber development. Phenylpropanoid concentrations were highest in immature tubers, as were some transcript levels and enzyme activities including phenylalanine ammonia lyase (PAL). Phenylpropanoid concentration differences between mature and immature tubers varied by genotype but in some cases were approximately threefold. The most abundant phenylpropanoid was chlorogenic acid (5CGA), which decreased during tuber maturation. Hydroxycinnamoyl-CoA:quinate hydroxycinnamoyl transferase (HQT) transcripts were highly expressed relative to other phenylpropanoid genes, but were not well correlated with 5CGA concentrations ($R^2=-0.16$), whereas HQT enzyme activity was. In contrast to 5CGA, less abundant chlorogenic isomers increased during development.

Concentrations of hydroxycinnamic acid amides were higher in immature tubers, as was expression of arginine and ornithine decarboxylases. Expression of several genes involved in carbohydrate or shikimate metabolism, including sucrose synthase and 3-deoxy-D-arabino-heptulosonate 7-phosphate (DAHP), showed similar developmental patterns to phenylpropanoid pools, as did shikimate dehydrogenase enzyme activity. Sucrose, glucose and fructose concentrations were highest in immature tubers. Exogenous treatment of potatoes with sugars stimulated phenylpropanoid biosynthesis, suggesting sugars contributed to the higher phenylpropanoid concentrations in immature tubers.

A total of 62 HCAs (hydroxycinnamic acids)/its conjugates HCAs (chlorogenic acid, cryptochlorogenic acid and neochlorogenic acid)/DHCAs (dihydrohydroxycinnamic acid conjugates) were found in extracts from peel and flesh of 15 Columbian potato cultivars (Narváez-Cuenca et al. 2013). Among them, only twelve compounds were common to all cultivars in both peel and flesh. The less commonly described compounds accounted for 7.1–20.1 % w/w of the total amount of HCAs/HCAcs/DHCAs in whole tubers, highlighting their contribution to the total phenolic profile of potato tubers. Among the 15 Columbian cultivars, the abundance (mg/100 g DW whole tuber) of neochlorogenic acid (0.8–7.4 mg) ranged in similar quantities as the less commonly reported feruloyl octopamine (1.2–5.2 mg), 5-*O*-feruloyl quinic acid (0.1–7.5 mg), *cis*- chlorogenic acid (1.1–2.2 mg), caffeoyl putrescine (0.6–2.5 mg), sinapoyl hexose (0.1–1.8 mg), *N*^l,*N*¹⁴-*bis*-(dihydrocaffeoyl)spermine (0.2–1.7 mg), *N*^l,*N*¹⁰-*bis*-(dihydrocaffeoyl)spermidine (1.1–2.6 mg) and *N*^l,*N*⁵,*N*¹⁴-*tris*-(dihydrocaffeoyl)spermine (trace, 11.1 mg). A total of 31 compounds were identified and quantified in a white potato cultivar and a purple potato cultivar, Urenika, extracts (Chong et al. 2013). The compounds included several types of anthocyanins, hydroxycinnamic acid (HCA) derivatives and hydroxycinnamic amides (HCAA). Six classes of compounds, namely, organic acids, amino acids, HCA, HCAA, flavonols and glycoalkaloids, were present in both

extracts, but quantities varied between the two extracts.

Monomeric anthocyanin content in red-fleshed potatoes (*Solanum tuberosum* and *S. stenotomum*) ranged from 2 to 40 mg/100 g tuber fresh weight (Rodriguez-Saona et al. 1998). Two breeding clones, NDOP5847–1 and NDC4069–4, showed anthocyanin content >35 mg/100 g. All red potato samples showed similar pigment profiles, with pelargonidin-3-rutinoside-5-glucoside acylated with *p*-coumaric acid being the major anthocyanin (ca 70 %). The presence of glycoalkaloids in colour extracts was also detected. Some red-fleshed potatoes may be good potential sources of food colourants.

Anthocyanin content was as high as 150 mg cyanidin-3-glucoside equivalent/100 g (*Solanum stenotomum* subsp. *stenotomum*), and total phenolic content ranged from 110 mg (*S. stenotomum* subsp. *goniocalyx*) to 5120 mg (*S. tuberosum* subsp. *andigenum*) of GAE/100 g DW in 20 varieties of native Andean potatoes from 4 different *Solanum* species of different colours (Guisti et al. 2014). The presence of chlorogenic, caffeic, coumaric, ferulic, sinapic, gallic and protocatechuic acids had been reported in potatoes (Rodriguez-Saona et al. 1998; Lewis et al. 1998a; Reddivari et al. 2007a, b). Recently, Guisti et al. (2014) identified that the following phenolic compounds were tyrosine, 3-*O*-caffeoylquinic acid, chlorogenic acid, 4-*O*-caffeoylquinic acid, caffeic acid and quercetin–rutinoside derivative. Three anthocyanidins were identified in red potato extracts (cyanidin, pelargonidin and peonidin) and four anthocyanidins identified in the saponified samples of red potato extracts (cyanidin-3-rutinoside-glucoside, pelargonidin-3-rutinoside-5-glucoside (predominant), peonidin-3-rutinoside-5-glucoside and pelargonidin-3-rutinoside) (Guisti et al. 2014). Major anthocyanins identified in the red potato extracts were pelargonidin-3-rutinoside-5-glucoside, pelargonidin-3-caffeoyl-rutinoside-5-glucoside, petunidin-3-caffeoyl-rutinoside-5-glucoside, petunidin-3-*p*-coumaroyl-rutinoside-5-glucoside, pelargonidin-3-*p*-coumaroyl-rutinoside-5-glucoside, peonidin-3-*p*-coumaroyl-rutinoside-5-glucoside, pelargonidin-3-ferruloyl-rutinoside-5-glucoside and petunidin-3-ferruloyl-

rutinoside-5-glucoside. Five major anthocyanidins were identified in purple potato extracts: cyanidin, petunidin, pelargonidin, peonidin and malvidin. Petunidin and peonidin were the most predominant anthocyanidins in purple potato extract. Anthocyanidins identified in saponified purple potato extracts were cyanidin 3-rutinoside-5-glucoside, petunidin-3-rutinoside-5-glucoside, pelargonidin-3-rutinoside-5-glucoside, petunidin-3-rutinoside-5-glucoside and malvidin-3-rutinoside-5-glucoside. Eight major anthocyanins were identified in purple potato extracts: petunidin-3-caffeoyl-rutinoside-5-glucoside, cyanidin-3-*p*-coumaryl-rutinoside-5-glucoside, petunidin-3-*p*-coumaryl-rutinoside-5-glucoside, petunidin-3-ferruloyl-rutinoside-5-glucoside, pelargonidin-3-*p*-coumaryl-rutinoside-5-glucoside, peonidin-3-*p*-coumaryl-rutinoside-5-glucoside, malvidin-3-*p*-coumaryl-rutinoside-5-glucoside and peonidin-3-ferruloyl-rutinoside-5-glucoside.

Anthocyanin composition of coloured sections of potato tubers of genotypes CO97216-3P/PW comprised ten detectable anthocyanins, pelargonidin-3-*p*-coumaroylrutinoside-5-glucoside, cyanidin-3-*p*-coumaroylrutinoside-5-glucoside, peonidin-3-*p*-coumaroylrutinoside-5-glucoside, petunidin-3-*p*-coumaroylrutinoside-5-glucoside, malvidin-3-*p*-coumaroylrutinoside-5-glucoside, malvidin-3-*o*-caffeoyl-rutinoside-5-glucoside, delphinidin-3-*p*-coumaroylrutinoside-5-glucoside, petunidin-3-*o*-caffeoyl-rutinoside-5-glucoside, malvidin 3-rutinoside-5-glucoside and petunidin 3-rutinoside-5-glucoside, but two components, malvidin-3-*p*-coumaroylrutinoside-5-glucoside (trivial name negretetin) and petunidin-3-*p*-coumaroylrutinoside-5-glucoside (trivial name petanin), predominated (Stushnoff et al. 2010). The non-pigmented section also accumulated anthocyanins, but to a much lesser degree. The ratio of accumulation of individual anthocyanins varied between 2.5-fold higher for the minor components to 20-fold higher for the dominant anthocyanins. The anthocyanin content was, on average, 6.7-fold higher in the pigmented tissues. The pigmented tissues also had approximately 2.5-fold higher levels of chlorogenic acid than the non-pigmented sections suggesting a

general increase in phenolic components. However, the levels of two other major phenolic components, feruloyl and caffeoyl putrescine, were not significantly different. There were also no significant differences in ascorbate or glutathione levels or indeed in their oxidation state. However, the major glycoalkaloids, solanine and chaconine, were elevated in the purple tissue over the non-pigmented tissues. The pigmented genotypes Purple Majesty (PM), Mountain Rose (MRR), CO97216-1P/P (216) and CO97226-2R/R (226) had higher anthocyanin and total phenol contents than the non-pigmented genotypes. The red genotypes, MR and 226, contained mainly pelargonidin-3-*p*-coumaroylrutinoside-5-glucoside, whereas the purple genotypes, PM and 216, contained a wider range of anthocyanins, but petunidin- and malvidin-3-*p*-coumaroylrutinoside-5-glucoside derivatives predominated. It was notable that only 216 contained appreciable amounts of peonidin-3-*p*-coumaroylrutinoside-5-glucoside. The higher total phenol content was reflected in the levels of the major polyphenolic component of potato tubers, chlorogenic acid, which was substantially higher in the pigmented genotypes (216, 226, PM and MRR) than the non-pigmented genotypes. However, this trend did not apply to all polyphenolic components as illustrated by the levels of detectable hydroxycinnamic amine derivatives. Two pigmented genotypes (216 and 226) had considerably elevated levels of glycoalkaloids compared with other genotypes.

The biosynthetic pathway for anthocyanins, caffeoylquinates and other major phenolic derivatives (tyrosine, caffeoylputrescine, feruloyl putrescine) in potato tuber were schematically described by Stushnoff et al. (2010). The enzymes involved in the biosynthesis of anthocyanins pelargonidin from dihydrokaempferol were dihydroflavonol reductase (DFR), anthocyanin synthase (AS) and UDP-glucose:3-*O*-flavonoid glucosyltransferase (GFG); from dihydroquercetin to cyanidin were DFR, AS and GFG and from cyanidin to peonidin anthocyanidin-glycoside-3'-*O*-methyl transferase (AGMT); from dihydromyricetin to delphinidin were DFR, AS and GFG and from delphinidin to petunidin AGMT; and

from petunidin to malvidin AGMT. The enzymes involved in anthocyanin glycosylation were anthocyanidin-3-*O*-glycosyl transferase (A3GT), anthocyanidin-5-*O*-glycosyl transferase (A5GT) and UDP-glucose:3-*O*-flavonoid glucosyltransferase (GFG). AGA (anthocyanidin-3'-*O*-glycoside-6'-*O*-acyl transferase) incorporated anthocyanin glycosides with hydroxycinnamoyl groups. Other enzymes involved in the biosynthesis of caffeoylquinates and other major enzymes were aroenate dehydratase (ADT), chalcone isomerase (CHI), chalcone synthase (CHS), cinnamate-4-hydroxylase (C4H), 4-coumarate ligase (4CL), chorismate mutase (CM), flavonone-3-hydroxylase (F3H), ferulate 5-hydroxylase (F5H), flavonoid-3'-hydroxylase (F3'H), flavonoid-3',5'-hydroxylase (F3'5'H), flavonol synthase (FLS), hydroxycinnamoyl-CoA:shikimate hydroxycinnamoyl transferase (HCT), hydroxycinnamoyl-CoA:quinate hydroxycinnamoyl transferase (HQT), phenylalanine ammonia lyase (PAL), prephenate dehydratase (PDH) and putrescine N-hydroxycinnamoyl transferase (PHT). Also, common genes that were differentially expressed both in the purple versus white sector included caffeoyl-CoA *O*-methyltransferase, leucoanthocyanidin dioxygenase, glutathione *S*-transferase, dihydroflavonol 4-reductase, cytochrome *b5*, cytochrome *b5* DIF-F, MYB transcription factor MYB73, salicylic acid-binding protein 2, specific tissue protein 2, organ-specific protein S2, flavanone 3 β -hydroxylase, lipase class 3, anthocyanin 1, putative orcinol *O*-methyltransferase, cytochrome P450, phosphoprotein phosphatase, putative disease resistance protein and epoxide hydrolase I (Stushnoff et al. 2010).

Studies showed that concentrated culture filtrate (CCF) of *Phytophthora infestans* but not lipopolysaccharides (LPS) from *Pectobacterium atrosepticum* induced differential accumulation of major phenolics chlorogenic acid, phenolamides and flavonols including rutin (quercetin-3-*O*-rutinoside) and nicotiflorin (kaempferol-3-*O*-rutinoside) among 5 potato cultivars (Kröner et al. 2012). Total phenolics were related with resistance to *P. atrosepticum* but not to *P. infestans*. However, nicotiflorin was

inversely related with resistance to both pathogens. Rutin, but not nicotiflorin, inhibited pathogen growth in-vitro at physiological concentrations.

Fresh cutting of five long-term-stored potato cultivars (Agria, Cara, Liseta, Monalisa and Spunta) induced the biosynthesis of three flavonols, quercetin 3-rutinoside, quercetin 3-diglucoside and quercetin 3-glucosylrutinoside (Tudela et al. 2002). The flavonols were detected after a lag period of 3 days of cold storage. The content ranged from 6 to 14 mg/100 g of fresh weight depending on the cultivar after 6 days of storage. Chlorogenic acid as the main caffeic acid derivative and the amino acids, tyrosine and tryptophan were also quantified. The flavonol induction was higher in fresh-cut potatoes stored under light than in the dark. Domestic cooking such as boiling, microwaving and frying provoked a partial loss of the flavonols, which were retained in the range of 4–16 mg per serving (213 g). Steam cooking resulted in the highest retention of caffeic acid derivatives and aromatic amino acids compared with the other cooking methods studied. The results implied that due to the large amount of potatoes consumed in the Western diet, fresh-cut potatoes could be a significant source of health-promoting phenolics. For the pigmented potatoes, cooking heating treatment did not cause any changes in the phenolic acids content, while anthocyanins showed only a small decrement (16–29 %) (Mulinacci et al. 2008). The cv. Highland Burgundy Red showed anthocyanins and phenolic acid concentrations close to 1 g/kg and more than 1.1 g/kg, respectively. Vitellotte Noire showed the highest amounts of resistant starch. Potato starch digestibility and % of resistant starch, considered as a component of dietary fibre, were affected both by cultivar and by heating/cooling treatments.

Potato Suberin and Waxes

Suberin a cell-wall biopolymer with aliphatic and aromatic domains had been reported to consist a fatty acid polyester with esterified ferulic acid (Serra et al. 2010). In potato, ferulic acid esters were also the main components of periderm wax. Suberin and waxes embedded in the suberin

polymer were reported to be key compounds in the control of transpiration in the tuber periderm of potato. They reported a potato gene encoding a fatty ω -hydroxy acid/fatty alcohol hydroxycinnamoyl transferase (FHT), which was involved in the biosynthesis of suberin and suberin-associated wax in the biosynthesis of suberin and suberin-associated wax. Suberin in potato wound periderm was known to be a polyester containing long-chain fatty acids and phenolics embedded within the cell wall (Yan and Stark 2000). Carboxyl-labelled phenylalanine precursors provide evidence for the concurrent development of phenolic esters and of monolignols typical of lignin. Experiments with ring-labelled phenylalanine precursors demonstrate a predominance of sinapyl and guaiacyl structures among suberin's phenolic moieties. It was found that the insoluble intermediates of suberin biosynthesis indicated probable covalent linkages between moieties of its polyester and polysaccharide domains. Bernards and Razem (2001) described a hydrogen peroxide-generating system with NAD(P)H-dependent oxidase-like properties associated with the oxidation of hydroxycinnamic acids (and their derivatives) in the formation of potato suberin poly(phenolics) during suberisation. Native and wound periderm of potato tuber contained up to 20 % extractable lipids (waxes) (Schreiber et al. 2005). Besides linear long-chain aliphatic wax compounds, alkyl ferulates were detected as significant constituents. In wound periderm they amounted to more than 60 % of the total extracts. Within 1 month of storage, suberin amounts in the polymer increased twofold in native periderm (180 $\mu\text{g}/\text{cm}^2$), whereas in wound periderm about 75.0 $\mu\text{g}/\text{cm}^2$ suberin polymer was newly synthesised. Among the isolated fragments from controlled hydrolysis of the suberin aliphatic or aromatic domains were two hydroxyphenyl derivatives reported previously in lignins and a novel aliphatic–aromatic ester trimer (Arrieta-Baez and Stark 2006). Together these protocols helped to characterise the carbohydrate types that were bound covalently to the suberin polyester and to identify the interunit covalent linkages among the aliphatic ester, phenolic and carbohydrate moieties in suberised potato tissue.

Depolymerisations of potato suberin by cutinase-catalysed hydrolysis produced higher proportions of aliphatic monomers than hydrolysis with the NaOMe procedure (Järvinen et al. 2009). Monomers released by the two methods were mainly α , ω -dioic acids and ω -hydroxy acids, but the ratios of the detected monomers were different, at 40.0 and 32.7 % for methanolysis and 64.6 and 8.2 % for cutinase, respectively. The most abundant monomeric compounds were octadec-9-ene-1,18-dioic acid and 18-hydroxyoctadec-9-enoic acid, which accounted for ca. 37 and 28 % of all monomers, respectively. A suberin-enriched fraction, molecular weight (MW)=ca. 44×10^3 g/mol, silated from potato, was found to be a mixture of carbohydrates and polyesters of aliphatic long-chain hydroxy fatty acids and diacids linked via ester bonds to the phenolics, MW=ca. 27×10^3 g/mol, formed by guaiacyl and *p*-hydroxyphenyl structures (Mattinen et al. 2009). Phenolics in potato peels may be important sources of antioxidants for various applications.

Composition of periderm wax of potato tuber was reported as hydrocarbon 31 %, wax ester 7 %, fatty alcohol 24 %, fatty acid 11 % and unknown 27 % (Espelie et al. 1980). Chain-length distribution of the fatty alcohols, fatty acids, ω -hydroxy acids and dicarboxylic acids in the polar fraction of the chloroform extract of potato tuber were fatty alcohols C_{16} (0.03 %), C_{18} (0.03 %), C_{20} (0.02 %), C_{22} (0.01 %), C_{24} (0.02 %), C_{26} (0.05 %) and C_{28} (0.05 %); fatty acids C_{16} (0.04 %), C_{18} (0.03 %), C_{20} (0.02 %), C_{22} (0.03 %), C_{24} (0.04 %), C_{26} (0.05 %) and C_{28} (0.05 %); ω -hydroxy acids C_{22} (0.01 %) and C_{24} (<0.01 %); and dicarboxylic acids C_{22} (<0.01 %) and C_{24} (<0.01 %). Substance classes detected in chloroform/methanol extracts of native and wound periderm of potato tuber were linear long-chain aliphatic compounds (alkanes, alcohols and carboxylic acids) and aromatic compounds (mainly esters between primary alcohols and ferulic acid and, in traces, caffeic acid and feroyltyramine) (Schreiber et al. 2005). In native periderm the aromatic fraction amounted to about two-thirds of the aliphatic fraction after 28 days. In wound periderm aliphatic and aromatic fractions were

present in equal amounts up to 21 days. Carboxylic acids in ferulic acid esters had chain lengths ranging from C₁₆ to C₃₂ with the chain lengths C₁₆, C₁₈, C₂₁, C₂₃, C₂₈ and C₃₀ dominating. The suberin content of native periderm increased with storage time (0–28 days) from 100 to 180 µg/cm². The amount of newly forming wound periderm reached 75 µg/cm² after 30 days. Substance classes detected consisted of linear long-chain aliphatic compounds (alcohols, carboxylic acids, α,ω-dicarboxylic acids, ω-hydroxy acids and 2-hydroxy acids) and of aromatic compounds (coumaric, ferulic and anisic acids). In both native and wound periderm, chain lengths of 2-hydroxy fatty acids slightly decreased during storage time.

The principal components of potato leaf cuticular waxes were very long-chain n-alkanes, 2-methylalkanes and 3-methylalkanes (3.1–4.6 µg/cm²), primary alcohols (0.3–0.7 µg/cm²), fatty acids (0.3–0.6 µg/cm²) and wax esters (0.1–0.4 µg/cm²) (Szafranek and Synak 2006). The most abundant hydrocarbons were n-hentriacontane, 2-methyltriacontane, n-nonacosane and n-heptacosane. The relative composition of the alkanes was very similar in the four cultivars. The major primary alcohols were 1-tetracosanol (12–18 % of the total 1-alkanols), 1-hexacosanol (39–42 %) and 1-octacosanol (24–29 %). The distribution pattern was very similar in all four potato varieties. The most abundant fatty acids were tetracosanoic acid (32–46 % of the total fatty acids) and hexacosanoic acid (19–25 %). Three of the potato varieties displayed similar distributions of fatty acid homologues, but the Perkoz contained a relatively higher percentage of triacontanoic acid (20 %). A homologous series of very long-chain secondary alcohols was identified in the potato leaf waxes. The fragmentation patterns of the mass spectra of native 2-alkanols derived from potato waxes were similar to those of the 2-hexadecanol and 2-tricosanol standards. The sterol fraction consisted of two constituents only, cholesterol (1–60 ng/cm²) and β-sitosterol; the terpenoid β-amyrin was also found. A homologous series of methyl ketones (2-ketones, alkan-2-ones) with chain lengths from C₂₅ to C₃₃ was

present in the potato waxes. Potato methyl ketones were accompanied by ketones with the carbonyl group in positions 8, 10, 12, 14 and 16 as follows: nonacosanone, nonacosane-8-one, nonacosane-10-one, nonacosane-12-one and nonacosane-14-one; hentriacontanone, hentriacontan-8-one, hentriacontan-10-one, hentriacontan-12-one, hentriacontan-14-one and hentriacontan-16-one; tritriacontanone, tritriacontan-8-one, tritriacontan-10-one, tritriacontan-12-one, tritriacontan-14-one and tritriacontan-16-one. Potato waxes also contained detectable levels of very long-chain C₂₂ to C₃₂ aldehydes (13–17 ng/cm²). The most abundant of these were tetracosanal, hexacosanal, octacosanal and triacontanal. The distribution patterns of individual aldehydes were all quite similar in three of the four potato varieties studied; the exception was the Perkoz variety, which contained larger amounts of triacontanal and less hexacosanal. Homologous esters of very long-chain fatty acids with long primary alcohols (wax esters) were present in the cuticular waxes of the four potato varieties, but at different levels. The wax ester constituents were saturated straight-chain fatty acids and primary alcohols from C₁₄ to C₂₈ and from C₂₀ to C₂₈, respectively. The main esters were those of hexadecanoic (ca. 20 %), octadecanoic (10 %), eicosanoic (30 %), docosanoic (15 %) and tetracosanoic (8 %) acids. The distribution patterns of the fatty acids in the wax esters differed from those of the free fatty acids in potato waxes. The alcohols liberated from the wax esters consisted predominantly of docosanol (ca. 17 %), tetracosanol (20 %), hexacosanol (30 %) and octacosanol (15 %). Also present were benzoic acid esters and methyl, ethyl, isopropyl and 2-phenylethyl esters of fatty acids. Benzoic acid hexacosanyl, tetracosanyl and pentacosanyl esters predominated in the potato waxes. Potato waxes from all four varieties contained methyl esters of the even-carbon-numbered acids from C₁₆ to C₂₆ with yields from 2 to 8 ng/cm². Besides the methyl esters of saturated fatty acids, methyl linoleate and methyl linolenate were also present. The most prominent methyl esters were those of low molecular weight fatty acids (C₁₆:0, C₁₈:2, C₁₈:3, C₁₈:0). In addition,

ethyl esters of saturated fatty acids (C16–C26)—mainly the ethyl esters of hexadecanoic, octadecanoic, eicosanoic and tetracosanoic acids—were found as minor components.

Phytohormones and Endogenous Tuber-Inducing Compounds

Potato plant had been reported to contain phytohormones like jasmonic acid, auxins (IAA), gibberellins (GA), cytokinins, abscisic acid (ABA), ethylene and strigolactones. The involvement of all major classes of endogenous hormones in potato tuber dormancy was reviewed by Suttle (2004b). Based on available evidence, it was concluded that both ABA and ethylene were required for dormancy induction, but only ABA was needed to maintain bud dormancy. An increase in cytokinin sensitivity and content appeared to be the principal factors leading to the loss of dormancy. Changes in endogenous IAA and GA content appeared to be more closely related to the regulation of subsequent sprout growth.

Cytokinin-like substances were found in potato tubers near the end of their innate dormant period (Engelbrecht and Bielinska-Czarnecka 1972). Alcoholic extracts of potato tubers were found to contain cytokinins which could be separated from endogenous growth inhibitors (Antis and Northcote 1975). Three cell division inducing cytokinin compounds were extracted from sprouting potato tubers (Van Staden 1976). They were identified as zeatin riboside, isopentenyladenosine and isopentenyladenine. The main cytokinin detected in the water-soluble fraction of potato tuber was identified as zeatin ribotide (Koda 1982). The level of butanol-soluble cytokinin in elongating stolon tips was low, while that of water-soluble cytokinin was extremely high. Upon swelling of the stolon tips, the former increased greatly as the latter decreased. Following fractionation by HPLC, a total of eight endogenous cytokinins were detected in potato cv. Russet Burbank tuber apical bud tissue, and these were zeatin riboside-5'-monophosphate (ZRMP), zeatin-O-glucoside (ZOG), zeatin (Z), zeatin riboside (ZR), isopentenyl adenosine-5'-monophosphate (IPMP), isopentenyl adenine-9-glucoside (IP-9-G), isopentenyl adenine (IP) and

isopentenyl adenosine (IPA) (Suttle 1998b). Regardless of postharvest storage temperature or endodormancy status, IP-9-G was the most abundant cytokinin detected, while ZRMP and ZOG were the least abundant ones. In tubers preincubated at a growth-permissive temperature (20 °C) prior to extraction, the loss of endodormancy was preceded by significant increases in the endogenous levels of Z, ZR, IPMP and IP-9-G. When stored continuously at a growth-inhibiting temperature (3 °C), significant increases in ZR, IP-9-G and IP + IPA were observed. The total content of cytokinins increased by over sevenfold during postharvest storage, and this increase was a result of de novo biosynthesis.

Potato tubers stored in 80 % O₂ and 12 % CO₂ produced ethylene at much higher rates (Creech et al. 1973). In all cases where sprouting occurred, the rate of ethylene production increased. Endogenous ethylene was found to be essential for the full expression of potato microtuber endodormancy, and its involvement may be restricted to the initial period of endodormancy development (Suttle 1998a).

Potato (cv. Russet Burbank) microtubers generated in-vitro from single-node explants contained substantial amounts (approximately 250 pmol/g fresh weight) of free abscisic acid (ABA) and were completely dormant for a minimum of 12 weeks (Suttle and Hultstrand 1994). Microtubers that developed in the presence of 10 tzm fluridone (FLD) contained considerably reduced amounts (approximately 5–25 pmol (g fresh weight) of free ABA and exhibited a precocious loss of dormancy. Suttle (1995) demonstrated that ABA was readily metabolised by potato tubers and that the principal route of catabolism consisted of the oxidative metabolism of ABA to phaseic and dihydrophaseic acids with minimal esterification to conjugated ABA. The results also suggest that a decline in endogenous ABA below a threshold level was not a prerequisite for the loss of potato tuber dormancy and the onset of sprout growth.

Immediately after harvest, the endogenous contents of gibberellins GA₁₉, GA₂₀ and GA₁ were relatively high (0.48–0.62 ng/g fresh weight) in potato tubers (Suttle 2004a). The con-

tent of these GAs declined between 33 and 93 days of storage. Internal levels of GA₁₉, GA₂₀ and GA₁ rose slightly between 93 and 135 days of storage reaching levels comparable to those found in highly dormant tubers immediately after harvest. Levels of GA₁₉, GA₂₀ and GA₁ continued to increase as sprout growth became more vigorous. Neither GA₄ nor GA₈ was detected in any tuber sample regardless of dormancy status. Dormant tubers exhibited a time-dependent increase in apparent GA sensitivity. The results did not support a role for endogenous GA in potato tuber dormancy release but were consistent with a role for GAs in the regulation of subsequent sprout growth.

Tuberisation in potato plants had been considered to be controlled both by tuberonic acid TA and its glucoside formed in leaves under short-day conditions (Koda and Okazawa 1988; Koda et al. 1988). The tuber-inducing compound from potato leaves was identified as 3-oxo-2-(5'-β-D-glucopyranosyloxy-2'-Z-pentenyl)-cyclopentane-1-acetic acid, and its aglycone was named as tuberonic acid (Yoshihara et al. 1989). The chemical structure of tuberonic acid (3-oxo-2-[5-hydroxy-2-cis-pentenyl]-cyclopentane-1-acetic acid), the aglycone of a potato tuber-inducing substance isolated from potato leaves, was closely related to that of jasmonic acid (Koda et al. 1991). Jasmonic acid and its methyl ester showed strong tuber-inducing activity (Koda et al. 1991, 1992a).

Jasmonic acid endogenous level in potato tubers with unsprouted buds was 325 ng/g dry weight, diminishing during sprouting to 164 ng (Castro et al. 1999). The high levels of jasmonic acid found in potato tuber buds in correlation with the capacity of this compound to induce radial expansion of the meristematic cells in the buds indicated the participation of jasmonic acid in the growth of these organs during the process of bud transformation into sprouts. Theobroxide a natural compound from the fungus *Lasiodiplodia theobromae* was found to have a significantly inductive effect on potato tuber formation in-vitro and in-vivo. The results suggested that the inductive effect of theobroxide on tuber formation is probably achieved by

stimulating jasmonic acid (JA) and tuberonic acid (TA) synthesis as it increased endogenous levels of JA and TA and lipoxygenase (LOX) activity.

No significant changes were found in free auxin (indole-3-acetic acid, IAA) level during dormancy of potato tubers stored at 4 °C followed by a rapid decrease during sprouting (Sukhova et al. 1993). It was found that IAA did not appear to have a significant effect on tuber dormancy, while cytokinins were probably necessary for sprouting initiation. Under non-inductive long-day (LD) conditions, the free auxin IAA concentration increased from the apex to the lower parts of the potato plant (Roumeliotis et al. 2012). Average IAA concentrations of 560, 2510 and 3250 pmol of IAA/g fresh weight (FW) were measured for the shoot apex, middle and basal part of the stem, respectively. Under LD conditions, the free auxin concentration in the stolon apical meristem (STAM) was 270 pmol/g FW. After a small initial decrease after the switch to SD (inductive) conditions on day 5 (70 pmol/g FW), IAA levels increased dramatically to a maximum of 1050 pmol/g FW on day 16, at which time the first tubers were observed. The tuber apex had the lowest concentrations of free IAA (110 pmol/g FW) but in similar concentration ranges to those in the perimedullary region (120 pmol/g FW) and the pith (170 pmol/g FW). The highest concentration of IAA was observed in the tuber heel (240 pmol). IAA levels of whole tuber samples were ~160 pmol/g FW, significantly less than at tuber swelling (1050 pmol/g FW). Strigolactones were detected in stolons of in-vivo growing potato plants, and the role these may play in tuberisation remained unclear. Strigolactones were measured for the first time in potato roots. Studies suggested that auxin and strigolactone had the capacity to modulate each other's levels and distribution in a dynamic feedback loop required for the coordinated control of axillary shoot branching (Gomez-Roldan et al. 2008; Hayward et al. 2009). The results of a recent study by Pasare et al. (2013) suggested that strigolactones could have an effect, solely or in combination with other phytohormones, in the morphology of potato plants and also in control-

ling stolon development and maintaining tuber dormancy.

Potato leaves were found to contain a high basal level of free and conjugated salicylic acid (Yu et al. 1997). HPLC of acidic compounds from potato leaves soluble in aqueous methanol showed the presence of salicylic acid, benzoic acid, ferulic acid, caffeic acid or cinnamic acid (Coquoz et al. 1998). Radiolabelling studies with untreated leaves showed that salicylic acid was synthesised from phenylalanine and that both cinnamic and benzoic acid were intermediates in the biosynthesis pathway. However, the natural occurrence of salicylic acid was not detected in the leaves of potato plants that had been grown under tuber-inducing conditions (short days) and had begun to form tubers (Koda et al. 1992b). The results appeared to exclude the possibility of the involvement of salicylic acid in the natural tuberisation of potato plants.

Alkaloids

Solanine was first reported in potato by Baup (1826) who found much higher levels in the sprouts than in the tuber. The major glycoalkaloids in the cultivated potato were reported to be α -, β - and γ -solanine and α -, β - and γ -chaconine, all six compounds having the same steroidal base (solanidine) but differing in the attached sugar molecule linked glycosidically (Bretzlöff 1971). Potato tubers contained glycoalkaloids, α -solanine and α -chaconine, and the aglycones, demissidine and solasodine (Cahill et al. 2010). A means of distinguishing solanidine and demissidine by formation of their respective 3 β -trifluoroacetates with trifluoroacetic anhydride was demonstrated using gas–liquid chromatography (King 1980). Two major steroid glycoalkaloids, in addition to α -solanine and α -chaconine, were isolated from leaves and aged tuber slices of potato, *Solanum tuberosum* var. Kennebec, which possessed the germplasm of *Solanum demissum* (Shih and Kuć 1974). They were glycosides of tomatidenol and were identified as α - and β -solamarine. The compounds were not found in tuber peel or freshly sliced Kennebec tubers or in 20 other cultivars. The total glycoalkaloid content of the aged potato slices increased dramati-

cally on ageing; α -solanine and α -chaconine both increased in these slices, but the greatest increase was in the former (Fitzpatrick et al. 1977). Appearing solely in the aged slices of potato Kennebec variety, α - and β -solamarine appeared early in the storage period and gradually decreased over the storage period. Analyses of the unaged slices indicated that the glycoalkaloid content and composition of the potato tubers was little affected by storage. Ageing of potato sprouts did not change their glycoalkaloid content.

The glycoalkaloids, aglycones and carbohydrate components found in *Solanum* species including *S. tuberosum* were reported by Woolfe and Poats (1987): glycoalkaloid α -solanine, its aglycone solanidine and carbohydrate components trisaccharide, solatriose (D-galactose, L-rhamnose, D-glucose); glycoalkaloid α -chaconine, its aglycone solanidine and carbohydrate component trisaccharide, chacotriose (D-glucose and 2 molecules of L-rhamnose); glycoalkaloid dehydrocommersonine, its aglycone solanidine and carbohydrate component tetrasaccharide, commertetrose (D-galactose and 3 molecules of D-glucose); glycoalkaloid demissine, its aglycone demissidine and carbohydrate component tetrasaccharide, lycotetraose (D-galactose, D-glucose, D-glucose, D-xylose); glycoalkaloid α -solamarine, its aglycone tomatidenol and carbohydrate component trisaccharide, solatriose (D-galactose, L-rhamnose, D-glucose); and glycoalkaloid β -solamarine, its aglycone tomatidenol and carbohydrate component trisaccharide chacotriose (D-glucose, 2 molecules of L-rhamnose). Glycoalkaloids β - and γ -solanines and β - and γ -chaconines were products of partial hydrolysis of the respective α -glycosides.

Solanidin glycosides (mg/kg FW) had been reported in all parts of potato plant. Highest concentrations were found in flowers 2150–5000 mg (Lampitt et al. 1943; Wood and Young 1974; Kozukue et al. 1987); flower petals 3060–4970 mg and calyces 4770–5710 mg (Kozukue et al. 1987); unripe berries 420–1080 mg (Boemer and Mattis 1924; Lampitt et al. 1943); young leaves 230–1000 mg (Wood and Young 1974; Kozukue et al. 1987); and sprouts 1950–17,700 mg (extremely high due to illumination of

sprouts) (Wood and Young 1974; Kozukue et al. 1987). Glycoalkaloid (TGA) content in the stolons ranged from 150–540 mg, roots 180–400 mg, stems 23–33 mg, growing tops 300–860 mg (Lampitt et al. 1943; Wood and Young 1974; Kozukue et al. 1987), and lateral stems 30–71 mg (Kozukue et al. 1987). There were normal levels of TGA (mg/100 g FW) in various tuber tissues: whole tuber 7.5 (4.3–9.7) mg, flesh 1.2–5 mg, skin 2–3 % of tuber 30–60 mg, peel 10–15 % of tuber 15–30 mg, bitter tuber 25–80 mg, and peel from bitter tuber 150–220 mg (Wood and Young 1974). TGA levels in small tubers of 10–40 g were high 96–448 mg (Verbist and Monnet 1979). Friedman and Dao (1992) reported TGA (α -chaconine and α -solanine) contents of different parts of the new NDA 1725 potato cultivar (mg/100 g of fresh weight) as follows: tubers, 14.7; main stems, 32.0; small stems, 45.6; roots, 86; leaves, 145; and sprouts, 997. The α -chaconine content of several other potato cultivars ranged from 1.17 to 13.5 mg/100 g of fresh weight and the corresponding α -solanine content from 0.58 to 5.9 mg/100 g of fresh weight. The corresponding values for potato berries were 22.1 and 15.9 mg/100 g of fresh weight, respectively. Friedman et al. (2003a, b) reported 12–543 mg/kg FW TGA content in potato peel. Potato peels, accounting for about one-seventh of the whole tuber weight, contained solanine and solanidine, respectively, at concentrations 2.5 and 6.2 times higher than the remaining tuber tissue or approximately 30 % of the total glycoalkaloid amount (Zitnak 1961). The outer 3 mm of the tuber contained approximately half of the TGA; however, it represented only 14 % of total potato weight. Free alkaloid solanidine was detected in concentrations up to 200 ppm or 33 % of the total glycoalkaloid level in bitter Netted Gem potatoes. Continuous illumination with 15- and 25-W incandescent light for 10 days increased glycoalkaloid content of peelings (12–14 % of tuber weight) in uncured potatoes by a factor of 3.2 and 2.8, respectively, while the corresponding factor for cured tubers was only 1.8 for both lights (Zitnak 1981). The peeled tuber portion (86–88 % of tuber weight) had negligible amounts of

glycoalkaloids, averaging about 1 mg per 100 g of fresh weight. The rise of glycoalkaloid levels in peels of uncured tubers was nearly linear to 164.7 mg/100 g (15 W light) with no indication of levelling off. Bushway et al. (1983) found raw peels to contain 1.30–56.67 mg/100 g peel (wet weight), α -chaconine and 0.5–50.16 mg/100 g peel (wet weight) α -solanine. Raw flesh from the same potatoes contained 0.02–2.32 mg/100 g flesh (wet weight) α -chaconine and 0.01–2.18 mg/100 g flesh (wet weight) of α -solanine.

The tubers of Polish potato cultivars were reported to contain between 12 and 159 mg/kg glycoalkaloids, German cultivars 20 and 220 mg/kg, American cultivars 20 to 130 mg/kg and British cultivars 36 to 142 mg/kg (Dale and Mackay 1994; Nowacki 2009). The average TGA content (α -solanine and α -chaconine combined) for the different Swedish domestic early potato varieties ranged from 51 to 221 mg/kg fresh weight (Hellenäs et al. 1995a). α -Solanine constituted on average between 35 and 41 % of the glycoalkaloids detected. The glycoalkaloid concentrations in individual samples were in the range 31–344 mg/kg. The variety Ulster Chieftain accounted for 88 % of the samples above 200 mg/kg. The established Swedish consumer potato variety Magnum Bonum was found to contain potentially toxic levels of the glycoalkaloids (α -solanine and α -chaconine) in the tubers, ranging from 61 to 665 mg/kg fresh weight with an average of 254 mg/kg (Hellenäs et al. 1995b). Sixty-six percent of the samples exceeded a temporary maximum residue limit of 200 mg/kg; 8 % were above 400 mg/kg. Peeling did not significantly remove the glycoalkaloids in tubers with a high content. Tömösközi-Farkas et al. (2006) reported that tested Hungarian potato varieties contained between 0.09 and 15 mg/100 g glycoalkaloids. The content of glycoalkaloids in the new varieties of potato was lower than the limit of the official food regulations. A cross-Canada survey of B5141-6³ potatoes grown at 12 locations showed a distinct bitter off-flavour found to be due to the presence of unusually high total glycoalkaloid content (TGA), mostly in excess of 20 mg per 100 g of fresh weight (Zitnak and Johnston 1970). Samples of check varieties

commonly grown in the selected locations, Kennebec, Irish Cobbler and Netted Gem, showed comparably low, normal TGA levels. Significant differences in tuber glycoalkaloid (TGA) content were found among five commercial varieties and B5141-6 grown at 39 different locations in 28 states in America (Sinden and Webb 1972). Line B5141-6 had the highest average TGA content, 29.3 mg/100 g in 1970 and 28.1 mg/100 g in 1971. Average TGA contents in 1970 of Kennebec, Russet Burbank, Katahdin, Irish Cobbler and Red Pontiac were 9.7, 7.9, 7.9, 6.2 and 4.3 mg/100 g, respectively. There were also significant location effects. Storage of potatoes at 5 °C increased the proportions of the 4-*O*- α -D-galactoside of calystegine B₂ and the trihydroxylated calystegine A₃ (Watson et al. 2000). The following ranges of total glycoalkaloid (α -chaconine and α -solanine) and calystegine (A₃ and B₂) levels were observed for the eight USA potato varieties (Atlantic, Dark Red Norland, Ranger Russet, Red Lasoda, Russet Burbank, Russet Norkota, Shepody and Snowden): dry flesh, 5–592 and 6–316 mg/kg; dry peel, 84–2226 and 218–2581 mg/kg; dry whole potatoes, 40–883 and 34–326 mg/kg; wet flesh, 1–148 and 1–68 mg/kg; wet peel, 12–429 and 35–467 mg/kg; and wet whole potatoes, 7–187 and 5–68 mg/kg (Friedman et al. 2003b). The two water-soluble nortropane alkaloids, calystegines A₃ and B₂, were found to be potent glycosidase inhibitors. The α -solanine content of Pakistani potato varies from 45.98 to 2742.60 mg/100 g of dry weight (DW) in peel and from 4.01 to 2466.56 mg/100 g of DW in flesh (Aziz et al. 2012). Similarly, α -chaconine content varied from 4.42 to 6818.40 mg/100 g of DW in potato peel and from 3.94 to 475.33 mg/100 g DW in flesh portion. The total glycoalkaloids (TGA) concentration varied from 177.20 to 5449.90 mg/100 g of DW in peel and from 3.08 to 14.69 mg/100 g of DW in flesh portion of all the potato cultivars tested. All the potato cultivars contained lower concentration of TGA than the limits recommended as safe, except two cultivars, namely, FD 8-3 (2539.18 mg/100 g of DW) and Cardinal (506.16 mg/kg). The dietary intake assessment of potato cultivars revealed that

Cardinal, FD 35-36, FD 8-3 and FD 3-9 contained higher amount of TGA in whole potato, although FD 8-3 only possessed higher content of TGA (154.93) in its flesh portion rendering it unfit for human consumption. Potato tubers of all somatic hybrids (except one clone) between tetraploid *Solanum tuberosum* cv. Dejima and the dihaploid clone ATDH-1 induced by another culture from *Solanum acuale*-T (acl-T) were found to contain four glycoalkaloids, namely, α -chaconine, α -solanine, α -tomatine and demissine derived from the fusion parents. The lack of α -tomatine in the remaining clone may be due to somaclonal variation (Kozukue et al. 1999). *S. tuberosum* tubers contained α -chaconine and α -solanine, whereas acl-T and ATDH-1 tubers were found to contain α -tomatine and demissine.

The content of solanidine glycosides (mg/kg fresh weight) of individually analysed small tubers of four *S. tuberosum* cultivars grown in pots in a glasshouse were determined as follows: Bintje range 73–88 mg, average 126 mg; AM 78-3778 range 321–1484 mg, average 721 mg; Arabesque range 95–265 mg, average 1155 mg; and Pimpernel 132–1287 mg, average 522 mg. The average solanidine glycoside content of field-grown mature-harvested tubers were Bintje 40 mg, AM 78-3778 360 mg, Arabesque 58 mg and Pimpernel 146 mg (Van Gelder et al. 1988).

Three samples of commercial chips 3 contained 9.5–72 mg TGA/100 g chips (Sizer et al. 1980). Removal of peel lowered TGA content in finished chips. Two types of fried peels contained more α -chaconine (2.18–92.82 mg/100 g cooked peel) and α -solanine (1.09–72.09 mg/100 g cooked peel) (Bushway et al. 1983). Four commercial potato peel products—wedges, slices, fried peels and baked-fried peels—contained 3.60–13.71 mg α -chaconine/100 g cooked product and 1.60–10.48 mg α -solanine/100 g cooked product. The major glycoalkaloids in fried, baked, microwaved and boiled potatoes were α -chacocine ranging from 0.04 to 97.9 mg/100 g product and α -solanine 0.04 to 48 mg/100 g product (Bushway and Ponnampalam 1981). A slight loss of TGA was observed with frying. TGA

contents (mg/100 g product) in various potato products reported were in baked jacket potato 99–113 mg, fried skins 567–1450 mg, frozen mashed potato 2–5 mg, frozen baked potato 80–123 mg, frozen chips 2–29 mg, canned peeled potato 1–2 mg, dehydrated potato flour 65–76 mg, dehydrated potato flakes 15–23 mg (Bushway and Ponnampalam 1981), frozen skins 65–121 mg (Bushway et al. 1983), boiled peeled potato 24–42 mg (Mondy and Gosselin 1988), and frozen fried potato 4–31 mg Bushway and Ponnampalam 1981; Saito et al. 1990). Commercial potato products, such as potato crisps, chips and tinned new potatoes, have been found to contain similar low levels <10 mg/100 g on equivalent fresh weight basis were within those accepted as safe by breeders of commercial potatoes. Friedman and Dao (1992) reported the following glycoalkaloid contents in freeze-dried French fries (0.08–0.84 mg/100 g of product), skins (3.1–20.3 mg/100 g of product), potato chips (2.4–10.9 mg/100 g of product) and potato pancake powders (4.5–6.5 mg/100 g product). In the UK, potato products, when calculated on an equivalent fresh weight basis, all contained <10 mg/100 g (Davies and Blincow 1984). They reported the following mean glycoalkaloid levels in potato: main crop 10.4 mg/100 g, UK earlies 11.3 mg/100 g and imported earlies 12.3 mg/100 g.

The most abundant glycoalkaloids in potato were reported as α -solanine and α -chaconine (Friedman and McDonald 1997). The cultivated potato (*Solanum tuberosum*) contained α -solanine and α -chaconine in the ratio of 0.3 to 0.8 (α -solanine to α -chaconine) (Friedman et al. 2003a). Glycoalkaloids (α -solanine and α -chaconine) had been reported to contribute flavour to potatoes but at higher concentrations (>200 mg/kg) caused bitterness (Friedman 2006). Potatoes containing over 0.02 % steroid glycoalkaloids are considered toxic to man, and at this concentration they would impart a distinctly bitter flavour (Kuc 1984). Arachidonic acid and eicosapentaenoic acids, two polyunsaturated fatty acids isolated from *Phytophthora infestans*, were found to be potent inhibitors of steroid glycoalkaloid (α -chaconine and

α -solanine) accumulation in potato. Both acids elicited the localised accumulation of sesquiterpenoids including rishitin, lubimin, phytuberin, phytuberol and solavetivone. Rishitin and lubimin generally comprised 85–90 % of the total sesquiterpenoids which accumulated. The steroid glycoalkaloids and sesquiterpenoids appeared to have a role in disease resistance to some fungal pathogens.

Potato tubers protected from light contained 0.05–0.65 mg/100 g α -solanine and 0.3–0.63 mg/100 g α -chaconine, and concentrations in leaf samples ranged from 0.64 to 22.6 mg α -solanine/100 g and 0.06 to 55.7 mg α -chaconine/100 g (Phillips et al. 1996). Shakya and Navarre (2008) reported more than 50 glycoalkaloids with solanidane or solanidane-like aglycones in wild and three cultivars of *S. tuberosum*. Basal glycoalkaloid (α -chaconine and α -solanine) levels in tubers varied between potato cultivars (Petersson et al. 2013). Wounding and light exposure, but not heat, increased tuber glycoalkaloid levels, and the relative response differed among the cultivars. Also, calystegine levels (A_3 , B_2 and B_4) in potato tubers varied between cultivars, with calystegine B_4 showing the most marked variation. However, the total calystegine level was not affected by wounding or light exposure. There was strong variation among potato cultivars with regard to postharvest glycoalkaloid increases, suggesting that the biosynthesis of glycoalkaloids and calystegines occurred independently of each other.

The tubers of 14 potato varieties were analysed for glycoalkaloids. The levels of glycoalkaloids in tubers of 14 potato varieties were all within the safe limits for human consumption (Uppal 1987). The peels of tuber contained about 60–70 % of the total glycoalkaloids present in the whole tuber. The levels of glycoalkaloids in leaves and tubers were correlated ($R^2=0.865$). There was a significant increase in the content of glycoalkaloids in peels of tubers exposed to sunlight. Glycoalkaloid contents increased at the rate of 1.9 mg/100 g fresh weight per day in peels of Kufri Jyoti tubers exposed to diffused sunlight. The principal glycoalkaloids α -solanine and α -chaconine were present in higher concen-

tration in the peel than in the flesh of 12 commercial varieties of Mexican potato varieties (Sotelo and Serrano 2000). The main alkaloid in the peel of the potatoes was α -chaconine comprising about 65–71 % of the total glycoalkaloids. The high concentration of α -chaconine in peel, which was more toxic than α -solanine, afforded more protection to the tuber against predators. Based on the results, the consumption of the 12 commercial varieties of Mexican potatoes did not represent any danger to human health. Of 27 Japanese potato varieties, May Queen and Sherry showed high contents of total glycoalkaloids (α -solanine, α -chaconine) (180 mg/kg and 320 mg/kg, respectively) among the raw potatoes of middle size (ca. 100 g) (Shimoi et al. 2007). In contrast, Inca Red showed the lowest content of 21 mg/kg. Higher contents of total glycoalkaloids were found in smaller potatoes. The content of total glycoalkaloids varied in the range of 48–350 mg/kg in the potatoes in commercial foods with peel.

The tubers of the early potato variety Aster, harvested in the first period, contained the highest amount of glycoalkaloids, while the tubers of the middle-late variety Bryza, harvested in the second and third periods, contained the lowest amount of glycoalkaloids (Pęksa et al. 2002). Peeling of tubers caused a decrease of α -solanine and α -chaconine contents in the investigated varieties. The highest amounts of glycoalkaloids and nitrates were removed during peeling, blanching and frying (Rytel et al. 2005). In the processed potatoes, the ratio of α -chaconine to α -solanine decreased. French fries ready for consumption contained only 3–8 % of the glycoalkaloids and 5–6 % of the nitrates found in the raw material. Significant decrease of glycoalkaloids, particularly α -solanine, and nitrate contents was observed during the process of potato chips production (Pęksa et al. 2006). The ratio of α -chaconine to α -solanine contents during potato processing was maintained at a similar level during the whole process and was about 2.5:1. The highest amounts of glycoalkaloids were removed during peeling, slicing, washing and frying, and the highest amounts of nitrates during peeling and frying.

Percival et al. (1996) found that regardless of cultivar, glycoalkaloid concentrations were increased after light exposure compared with initial concentrations. Average daytime irradiance during this period was 232 $\mu\text{mol}/\text{m}^2/\text{s}$. Glycoalkaloid concentrations fluctuated with time and continuous accumulation of glycoalkaloids with time was not demonstrated. Glycoalkaloid synthesis was maximal in the sequence pink-skinned cv. Kerrs Pink < white-skinned cv. Pentland Hawk < red-skinned cv. Desiree. Exposure to daylight altered the ratio of α -chaconine/ α -solanine in tubers of cv. Desiree but not those in cv. Pentland Hawk and Kerrs Pink. Glycoalkaloid concentrations in all cultivars were higher than the recommended food safety level; this was reached after 8 days in cv. Kerrs Pink and Desiree and at 13 days in Pentland Hawk. Coloured-fleshed potato varieties contained lower than 300 mg/kg DW of glycoalkaloids (Tajner-Czopek et al. 2012). Red-fleshed varieties contained 8 % higher glycoalkaloid content than blue-fleshed varieties. The highest changes of proportion between α -solanine and α -chaconine were in crisps. The peeling process decreased the glycoalkaloid content in tubers regardless of variety. The highest decrease of glycoalkaloid was found in crisps and French fries. The glycoalkaloid content in the boiled peeled potatoes was less than 9 mg/100 g, but in A, Montsana and Puebla varieties, both glycoalkaloids were absent. Potatoes of coloured-fleshed varieties studied were characterised by a low glycoalkaloid content at 5.47 mg/100 g (Rytel et al. 2013). The production of dehydrated potato dice influenced the decrease in glycoalkaloids content in potato products. The majority of glycoalkaloid compounds were removed during the peeling (70 %) and blanching process (29 %). Potato dice blanched at the highest temperature (85 °C) and pre-dried at 120 °C was characterised by the lowest quantity of glycoalkaloids content, whereas the highest content of these compounds was found in dice blanched potato at the lowest temperature (65 °C) and pre-dried at 120 °C. The blanching process had greater influence on the decrease in glycoalkaloids content than pre-drying process.

Nikolic and Stankovic (2003) reported an optimal solid–liquid–liquid system for hydrolytic extraction of solanidine, a steroidal aglycone, from potato vines. Solanidine hydrolytic extraction (DHE) of more than 98 % was achieved when 10 % (w/v) hydrochloric acid in 50 % (volume) methanol was the first liquid phase and chloroform was the second liquid phase. The yield of solanidine (q(S)) under these conditions was calculated to be 0.24 g/100 g of potato vines. A run yielded 98 mg of solanidine (86.7 % recovery from potato crude extract) in a one-step separation using centrifugal partition chromatography (CPC) (Attoumbré et al. 2013). The purity of the isolated solanidine was over 98 %. α -Chaconine (54 mg) and α -solanine (15 mg) were separated from crude potato extract in one step of purification using CPC (Attoumbré et al. 2012). A run yielded 98 mg of solanidine (86.7 % recovery from potato crude extract) in a one-step separation using centrifugal partition chromatography (CPC) (Attoumbré et al. 2013). The purity of the isolated solanidine was over 98 %. α -Chaconine (54 mg) and α -solanine (15 mg) were separated from crude potato extract in one step of purification using CPC (Attoumbré et al. 2012). Using response surface methodology, optimal ultrasound-assisted extraction (UAE) conditions resulted in the recovery of 1102 μ g steroidal alkaloids/g dried potato peel (DPP) (Hossain et al. 2014). In contrast, solid–liquid extraction (SLE) yielded 710.51 μ g/g glycoalkaloid DPP. Recoveries of individual glycoalkaloids using UAE yielded 273, 542.7, 231 and 55.3 μ g/g DPP for α -solanine, α -chaconine, solanidine and demissidine, respectively, whereas for SLE yields were 180.3, 337.6, 160.2 and 32.4 μ g/g DPP for α -solanine, α -chaconine, solanidine and demissidine, respectively.

The polyhydroxylated nortropane alkaloids called calystegines were found in the tubers and leaves of *Solanum tuberosum* (Nash et al. 1993). They were found to be potent inhibitors of glycosidases and may be responsible for neurological disorders in livestock. Calystegines A₃ and B₂ had been demonstrated to occur in the leaves, skins and sprouts of *S. tuberosum* (Asano et al. 1997). Calystegine B₂ was a strong competitive

inhibitor of the α -galactosidase activity in human and animal livers. Human β -xylosidase was inhibited by all four nortropanes calystegines A₃, B₁, B₂ and C₁. Calystegines A₃ and B₂ were found in various parts of the tubers (whole potato, peel, flesh and sprouts) (Kvasnicka et al. 2008; Griffiths et al. 2008). On average, calystegine concentrations in the peel were about 13 times that found in the flesh for the five *S. tuberosum* group Tuberousum cultivars (Griffiths et al. 2008). The calystegine content of sprouts of the four cultivars was found to include small amounts of four additional types, calystegine B₃, B₄, N₁ and X₂, in addition to the more abundant A₃ and B₂. Concentrations in the sprouts were on average 100 times higher than that in the tuber flesh and 8 times higher than in the peel. No correlation was found between sprout concentration and either flesh or peel calystegine concentration.

Volatiles and Miscellaneous Compounds

Potato flavour is a complex trait resulting from the presence of a combination of volatile and non-volatile compounds (sugars, glycoalkaloids, major umami amino acids and 5'-ribonucleotides) (Morris et al. 2011). Tuber-specific over-expression of a potato α -copaene synthase gene resulted in enhanced levels (up to 15-fold higher than controls) of the sesquiterpene α -copaene. A positive correlation ($R^2=0.8$) between transgene expression level and α -copaene abundance was observed. No significant changes in the levels of volatiles other than α -copaene were detected. Sensory analysis suggested that α -copaene was not a major component of potato flavour. There were strong correlations between umami compounds amino acids, glutamate and aspartate, and the 5'-nucleotides, guanosine monophosphate (GMP) and adenosine monophosphate (AMP) with flavour attributes and acceptability scores from a trained evaluation panel, suggesting umami to be important component of potato flavour (Morris et al. 2007). A range of non-volatile metabolites including the major umami compounds, glycoalkaloids and sugars in cooked potato tuber were found to impact on potato flavour (Morris et al. 2010). Correlation and princi-

pal component analyses revealed differences between the potato cultivars and storage conditions and demonstrated associations of metabolites with the different sensory attributes.

Studies by Burton and Meigh (1971) suggested that sprout inhibiting volatile constituent(s) of potato may be olefinic, ethereal and/or sulphur containing. Ethylene may be produced in very small quantities, insufficient to be an active olefinic constituent. Of the identified aromatic compounds evolved by stored potato tubers, benzothiazole, 1,4-dimethylnaphthalene and 1,6-dimethylnaphthalene were found to be comparatively potent inhibitors of sprout growth in the potato tuber (Meigh et al. 1973). The growth-suppressing activity of the two dimethylnaphthalenes was comparable with that of isopropyl-(*N*-3-chlorophenyl)-carbamate, used commercially in potato storage. Filmer and Rhodes (1984) found 1,4,6-trimethylnaphthalene to be an effective sprout suppressants compared to 1,4-dimethylnaphthalene; 1,4,5-trimethylnaphthalene; 2,3,6-trimethylnaphthalene; and 1,6,7-trimethylnaphthalene in bioassays based on both excised cultured shoot tips and intact potato tubers. Two volatile compounds produced by potato tubers with sprout growth-inhibitory activity was identified as diphenylamine and dibenzothiophene; the former was found to be an effective sprout suppressant for whole tubers (Filmer and Rhodes 1985). Treatment of nondormant potato tubers with vapours of six 8–10-carbon α,β -unsaturated carbonyl compounds suppressed sprout growth at 16 °C (95 % relative humidity) over ca. 3 months in storage in a concentration-dependent manner (Knowles and Knowles 2012). The volatile metabolites produced by sprout and associated tuber tissues following treatment with 3-octen-2-one, 3-nonen-2-one and 3-decen-2-one were the corresponding alkyl ketones and alkyl secondary alcohols. In contrast, (*E*)-2-octenal, (*E*)-2-nonenal and (*E*)-2-decenal were metabolised by two pathways: (1) parent compound to the corresponding alkyl aldehyde and then to the alkyl primary alcohol and (2) parent compound to the alkenyl primary alcohol. The concentrations of the parent ketone and aldehyde declined rapidly

following application, and the most persistent metabolites were 2-nonanol and (*E*)-2-nonen-1-ol, respectively.

2-Methoxy-3-isopropylpyrazine was found to be a major contributor to the earthy aroma of potato (Buttery and Ling 1973). Other volatile compounds identified included heptanol, octanol, octan-3-ol, hexan-2-one and non-*cis*-3-enol. Twelve volatile aroma compounds were found in potato tubers from different varieties after harvesting: two unknowns, acetaldehyde, propanal, 2-butanone, pentanal, hexanal, heptanone, *n*-heptanal, 2-hexenal, octanal and nonanone (Khan et al. 1977). The major volatile aroma compounds in potato tubers were identified as: *n*-pentanol, *n*-hexanol, (*E*)-2-hexenal, *n*-heptanal, (*E,E*)-2,4-decadienal and (*E,Z*)-2,4-decadienal (Fischer 1991). There were clear quantitative differences in the aromatic spectrum over a wide range of nitrogen and potassium inputs. Individual components altered within the spectrum especially after high nitrogen inputs. It was postulated that changes in the aroma of potato after increased fertiliser inputs were due to saturated and unsaturated aldehydes with their low sensory. Ulrich et al. (2000) identified the following volatiles in raw potato extract: 2,3-butanedione; 2,3-pentanedione; hexanal; 1-penten-3-ol; pyridine; 2-methyl-1-butanol; 2-pentylfuran; (*E*)-2-(1-pentyl)furan; 1-hexanol; (*E*)-2-octenal; 2-furancarboxaldehyde; (*E*)-2-nonenal; (*E,Z*)-2,6-nonadienal; phenylacetaldehyde; (*Z*)-3-nonen-1-ol; β -damascenone; 2,4-decadienal; benzyl alcohol; phenylethyl alcohol; pyrazine; methylpyrazine; 2,5-dimethylpyrazine; 2,6-dimethylpyrazine; 2-ethyl-6-methylpyrazine; 2,6-diethylpyrazine; 3-ethyl-2,5-dimethylpyrazine; 2-ethyl-3,5-dimethylpyrazine; and antioxidant activity and total phenolics in different genotypes of potato (*Solanum tuberosum* L.).

The following volatiles were emitted by potato foliage: *trans*-2-hexenal, 1-hexanol, 2-hexanol, 3-hexanol, *trans*-2-hexen-L-ol, *trans*-3-hexen-L-ol, *cis*-3-hexen-L-ol, *cis*-2-hexen-1-ol and linalool (Visser and Avé 1978; Visser et al. 1979). Bolter et al. (1997) identified the following volatiles in the head space of intact potato plants ((*Z*)-3-hexen-1-ol; nonanal; decanal; linalool;

4,8-dimethyl-1,3(*E*),7-nonatriene; β -caryophyllene; α -selinene; β -selinene; myrcene, limonene; ledol; δ -cadinene; γ -cadinene and α -pinene) and from Colorado beetle (*Leptinotarsa decemlineata*)-infested and damaged potato plants ((*Z*)-3-hexen-1-ol; (*Z*)-3-hexen-1-yl-butyrate, heptanal, octanal, nonanal, decanal, linalool, 4,8-dimethyl-1,3(*E*),7-nonatriene; 1,4,8-trimethyl-1,3(*E*),7-(*E*),11-decatraene; β -caryophyllene; α -selinene; β -selinene; selinene; 3-pentanone; sabinene; myrcene; limonene; methyl salicylate; ledol; α -cubebene; α -copaene; β -elemene; α -humulene; germacrene D; δ -cadinene; γ -cadinene; (*Z*)-3-hexen-1-yl acetate; β -sesquiphellandrene; (*E*)- α -bergamotene; indole; 1,8-cineole; furfural; γ -muurolene; ar-curcumen; tricyclene; (*E*)- β -farnesene; and α -pinene). Two cyclic sesquiterpenes, caryophyllene and germacrene D, were identified in the volatile secretions of potato leaves; caryophyllene was found to be a food attractant for potato Colorado beetle (Khalilova et al. 1997). Fourteen volatile sesquiterpenoids were identified in headspace samples collected from potato plants mechanically damaged or fed upon by the Colorado beetle larvae: β -caryophyllene, *trans*- α -bergamotene, sesquisabinene, α -humulene, (*E*)- β -farnesene, (-)-germacrene D, *trans*- β -bergamotene, α -zingiberene, bicyclogermacrene, (+)-germacrene A, β -sesquiphellandrene, germacrene D-4-ol, caryophyllene oxide and ledol (Weissbecker et al. 2000). The antennae of the predaceous stinkbug *Perillus bioculatus* responded to β -caryophyllene, α -humulene, (*E*)- β -farnesene, (-)-germacrene D and germacrene D-4-ol. Two sesquiterpenes that coeluted, α -zingiberene and bicyclogermacrene, together also elicited olfactory responses of *P. bioculatus*, whereas the individual compounds did not. Karlsson et al. (2013) proposed that volatiles, such as sesquiterpenes and aldehydes, mediated oviposition behaviour of the Guatemalan potato moth *Tecia solanivora* and were correlated with biosynthetically related, non-volatile compounds of potato tubers, such as steroidal glycoalkaloids, which influenced larval survival. Survival of larvae was negatively correlated with the tuber content of the steroid glycoalkaloids α -solanine and

α -chaconine: healthy potatoes contained lower amounts than stressed tubers, ranging from 25 to 500 $\mu\text{g/g}$ and from 30 to 600 $\mu\text{g/g}$, respectively. Analysis of volatile compounds emitted by potato tubers revealed that stressed tubers could clearly be distinguished from healthy tubers by the composition of their volatile profiles. Compounds that contributed to this difference were, e.g. decanal, nonanal, isopropyl myristate, phenylacetaldehyde, benzothiazole, heptadecane, octadecane, myristicin, *E,E*- α -farnesene and verbenone. Earlier they found that Guatemalan moth females showed a strong response to several sesquiterpenes and monoterpenes that were emitted from potato foliage only (Karlsson et al. 2009). Potato foliage of three phenological stages, from sprouting to tuberisation and flowering, released more than 30 sesquiterpenes which appeared to mediate host finding and oviposition in the Guatemalan moth. The main compounds were β -caryophyllene, germacrene D-4-ol, germacrene D, kunzeaol and (*E,E*)- α -farnesene. In addition, antennae responded to methyl phenylacetate, a floral fragrance that was released in large amounts from flowering plants and that was also present in potato tuber headspace. Female and male moths were attracted to methyl phenylacetate; this compound may accordingly contribute to female attraction to tuber-bearing potato plants in the field as well as to potato tubers in storage. Mated females of the potato tuberworm moth *Phthorimaea operculella* were attracted to volatiles released from intact potato tuber but unmated females did not (Arab et al. 2007). The polyphagous predator *Orius insidiosus* were attracted to volatiles from tubers damaged by *P. operculella* larvae, but did not respond to intact or mechanically damaged tubers. Methyl jasmonate (MeJA) was the only compound identified from the headspace of potato tubers. Behavioural bioassays with synthetic MeJA confirmed that the response of the insects is dependent on MeJA concentration.

The following volatiles were detected from potato tubers infected with *Erwinia carotovora*: acetone, ethanol, 2-butanone, acetaldehyde, methyl acetate, ethyl acetate, propanethiol, hydrogen sulphide, methyl sulphide, n-propanol

and isobutanol (Varns and Glynn 1979). The following volatiles were generated by potato tubers infected with *Erwinia carotovora*: acetone; 2-propenal; 2-methyl propanal; 2-butanone; acetic acid; 1 hexene; 1-butanol; 2-methylhexane; 2-pentanone; heptane; dimethyl sulphide; methylcyclohexane; toluene; hexanal; octane; octene; 2-methyl-octane; ethyl benzene; xylene; 3-methyl-octane; 1,2,3-trimethylcyclohexane; 1,2-dimethyl benzene; 1-methyl-2-propyl-cyclopentane; 1-heptene; 1-ethyl-4-methylcyclohexane; nonane; 2,4-dimethylhexane; propyl-cyclohexane; 1-ethyl-2-methylbenzene; phenol; 2-methyl-nonane; 3-methyl-nonane; octanal; trimethyl benzene; 2,2,3,4-tetramethyl-pentane; 1,2-undecadiene; decane; 4-methyldecane; limonene; (2-methylpropyl)-cyclohexane; 3-methyl-bicyclo[3.2.1]-oct-2-ene; 3-methyldecane; 5,6-dimethyl-decane; 1-methyl-4-(1-methyl)-ethyl benzene); nonanol; 3-methyl-1-heptene; naphthalene; decanal; 2-phenoxyethanol; long-chain aliphatic (heptadecane); butanoic acid; 1(3*H*)isobenzofuranone; long-chain aliphatic; hexacosane; 3,4-dimethyl-1-decene; 3-methylnonane and 1-hexacosanol (de Lacy Costello et al. 1999). The following volatiles were generated by potato tubers infected with *Bacillus polymyxa*: acetone, 2-methyl-pentane, acetic acid, hexane, but-1-ene, cyclohexane, 2-methyl-1-pentene, 2-methylhexane, 3-methylhexane, heptane, methylcyclohexane, *N,N*-dimethyl-formamide, toluene, hexanal, xylene, 1-ethyl-3-methyl-benzene, decanal, 2-phenoxyethanol, 1-pentadecene, phytol and 1-chloro-tetradecane (de Lacy Costello et al. 1999). The following volatiles were generated by potato tubers infected with *Arthrobacter* sp.: acetone; 2-methyl-pentane; acetic acid; hexane; but-1-ene; cyclohexane; 2-methyl-1-pentene; 2-methylhexane; 3-methylhexane; 2,3-dihydrofuran; 1,2-dimethyl-*cis*-cyclopentane; heptane; methylcyclohexane; toluene; octane; xylene; 1-ethyl-3-methyl-benzene; nonanal; decanal; 2-phenoxyethanol and hexacosane (de Lacy Costello et al. 1999). The following volatiles were generated by potato tubers inoculated with sterile distilled water: acetone; 2-propenal; 2-methyl-pentane; 3-methyl-

pentane; 2-butanone; acetic acid; hexane, 1-butanol; cyclohexane; 2-methyl-1-pentene; (*E*)-2-butene; 2-methylhexane; 2-pentanone; 2,3,-dimethyl-pentane; 3-methylhexane; 2,4-dimethylheptene; 1,2-dimethyl-*cis*-cyclopentane; (*E*)-2-butenal; heptane; methylcyclohexane; toluene; hexanal; octane; ethylbenzene; xylene; 3,4-dihydro-2*H*-pyran; 1,2-dimethyl benzene; nonane; 2,4-dimethyl-hexane; propylcyclohexane; 1-ethyl-2-methyl-benzene; phenol; 2-methyl-nonane; trimethyl benzene; 1-ethyl-3-methyl-benzene; decane; 4-methyldecane; limonene; (2-methylpropyl)-cyclohexane; 1-methyl-3-propyl-benzene; 2-methyldecane; 3-methyldecane; 1-methyl-4-(1-methyl)-ethyl benzene); 2,9-methyldecane; decanal; 2-phenoxyethanol; dodecane; 1(3*H*)isobenzofuranone; phytol; 3,4-dimethyl-1-decene; 3-methylnonane; 1-hexacosanol; 1-eicosanol; ((dodecyloxy)methyl)-oxirane; 3,5,24-trimethyl-tetracontane; and 1-chlorotetradecane (de Lacy Costello et al. 1999).

Schütz et al. (1999) found 2-ethyl-1-hexanol in significant amounts in the headspace of potato tubers infected by *Phytophthora infestans*. The following volatile compounds were collected from potato tuber inoculated with *Fusarium coeruleum* and *P. infestans* after incubation at 10°C for 42 days: acetone, 2-methyl propanal; butanal; acetic acid; 2-butenal; 3-methyl-butenal; 1-butanol; cyclohexane; 2-methylhexane; 2-methylhexane; heptane; acetamide; methylcyclohexane; 1-pentanol; *N,N*-dimethylformamide; toluene; hexanal; acetic acid butyl ester; 2-furancarboxaldehyde; *N,N*-dimethylacetamide; xylene; 2-heptanone; styrene; benzaldehyde; phenol; 2-pentylfuran; benzyl alcohol; 2-ethyl-1-hexanol; limonene; 2-octenal; acetophenone; 1-octanol; methyl benzoate; nonanal; undecane; naphthalene; *iso*-menthol; decanal; 2-phenoxyethanol; verbenone; dodecane; benzothiazole; tridecane; copaene; tetradecane; caryophyllene; *iso*-caryophyllene; *n*-dodecanol; pentadecane; hexadecane; butylated hydroxyl toluene; 2-methylpropanoic acid-2,2-dimethyl-1-(2-hydroxy-1-methylethyl)-propyl ester; and 2-methylpropanoic acid-3-hydroxy-2,4,4-trimethyl-pentyl ester (de Lacy Costello et al.

2001). The following volatile compounds were collected in the headspace of potato tuber inoculated with sterile distilled water after incubation at 10 °C for 42 days: acetone, acetic acid, 2-methyl propanal, 2-butenal, 1-butanol, cyclohexane, 2-methylhexane, methylcyclohexane, heptane, toluene, hexanal, xylene, phenol, limonene, decanal, 2-phenoxyethanol and dodecane (de Lacy Costello et al. 2001).

Volatiles generated from potatoes inoculated with *Ralstonia solanacearum*, pathogen of potato brown rot include 1-hepten-3-ol; 3,6-dimethyl-3-octanone; 3-ethyl-3-methyl-pentane; 1-chlorooctane; benzothiazole; 3-methylbutanoic acid; 2,2,3,4-tetramethyl-pentane; 2,3,4-trimethylhexane; 4 methyl-octane; and 4 methyl-2-propyl-1-pentanol (Blasiole et al. 2014). Volatiles generated from potatoes inoculated with *Clavibacter michiganensis* subsp. *sepedonicus* pathogen of potato ring rot disease include: 2-propanol, 3-methyl-3-buten-2-one and toluene. Possible volatile compounds are detected in the head space of *R. solanacearum* diseased tubers include: methanol, 2-propanol; acetaldehyde; 2-propane; acetic acid; ethyl acetate; dimethyl sulphide; 2-butanone; cyclohexane; hexanal; 3-methyl-3-buten-1-ol; 2,3-butanedione; 2 pentanone and dimethyl disulphide. Possible volatile compounds detected in the head space of *Clavibacter michiganensis* subsp. *sepedonicus* diseased tubers include: methanol, 2-propanol; acetaldehyde; ethanol; acetic acid; ethyl acetate; 2-butanone; cyclohexane; hexanal; 3-methyl-3-buten-1-ol; 2,3-butanedione; 2 pentanone and toluene.

A wide range of C₁–C₄ alcohols and carbonyls were identified in the volatile profile of *Erwinia carotovora*-infected potato tubers compared to healthy tubers (Waterer and Prtichard 1984). A total of 81 volatile metabolites were detected from Russet Burbank potatoes inoculated with *Erwinia carotovora* ssp. *carotovora* (ECC), *Erwinia carotovora* ssp. *atroseptica* (ECA) and *Fusarium sambucinum* (FSA), of which 58 were specific to one or common to a few but not to all inoculations/diseases (Liu et al. 2005). Acetic acid ethenyl ester was unique to ECA, while 1-methyl-4-(1-methylethenyl)-cyclohexene; dimethyl; 1,4-cyclohexadiene; and methoxy-(1,1-dimethyl-2-dihydroxy-ethyl)-amine were

unique to ECC, and 2,5-norbornadiene; 4-methyle-1-(1-methylethyl)-bicyclo[3.1.0]hexane; propylene oxide; trichloroethylene; and styrene were unique to FSA. Volatiles uniquely emitted by non-wounded non-inoculated tubers were dichloroacetonitrile, α -phenyl-benzeneacetaldehyde and fluoroethane, and volatile uniquely emitted by wounded non-inoculated tubers was 1,3-cyclopentadiene. The other volatile compounds included: 1,2-dimethoxy-ethene; 1-butanol; 2-methyl-1-butanol; 1-butanol, 2-methyl-, acetate; 1-butanol, 3-methyl-, acetate; 1-pentanol; 1-propanol; 3-hydroxy-2-butanone; acetic acid, 2-methylpropyl ester; acetic acid, methyl ester; acetone; borane-methyl sulphide complex; 2-methyl butanoic acid; ethyl ester butanoic acid; 2,2,3-trimethyl-cyclobutane; dimethyl trisulphide; ethanol; ethyl acetate; methyl ethyl disulphide; methyl ester pentanoic acid; thiirane; DL-3,4-dimethyl-3,4-hexanediol; 2,2-dimethyl-butane; 4-methylene-L-(1-methylethyl)-cyclohexene; azetidine; 4-methyl-1-(1-methylethyl)-bicyclo[3.1.0]hex-2-ene; bicyclo[4.1.0]hept-4-en-3-ol; 1-methyl-5-(1-methylethenyl)-cyclohexene; methyl hydrazine; dimethyl disulphide; 1,2,4-benzenetricarboxylic acid; 1-undecene; 2-methyl-5-(1-methylethyl)-bicyclo[3.1.0]hexan-2-ol; methyl nitrate; 2-methyl-2-propanamine; 1,3-dimethyl benzene; dimethyl ether; 1,4-dichlorobenzene; α ,4-dimethyl-benzenemethanol; methylene chloride; 1,2-dimethyl benzene; 6,6-dimethyl-2-methylene-bicyclo[3.1.1]heptane; 1-methyl-4-(1-methylethylidene)-cyclohexene; methylpropyl disulphide; *N,N*-dimethyl-1-butanamine; 2-butanone; 2-cyclopenten-1-one; 3-carene; 2-methyl-4,6-octadiyn-3-one; α -myrcene; α -phellandrene; α -pinene; 1,2-dichlorobenzene; 1,3-dichlorobenzene; 1-methyl-3-(1-methylethyl)-benzene; 1-methyl-4-(1-methylethyl)-benzene; 2-methyl-5-(1-methylethyl)-bicyclo[3.1.0]hex-2-ene; 1-methoxy-3-methyl butane; chloroform; dipropyl disulphide; ethylbenzene; formic acid; methyl-hydrazine oxalate (1:1); 1,3-cycloheptadien-1-lmethyl ketone; limonene, *p*-xylene; and trichloromonofluoromethane.

Black spot-related pigments were partially purified from bruised tubers of two commercial

potato cultivars (cv. Bildtstar and cv. Lady Rosetta) (Stevens and Davelaar 1996). Chemical characterisation showed that these pigments consisted of protein and a relatively small amount of covalently bound constituents. They did not contain eumelanin. Quinic acid was detectable in hydrolysates of the pigments from Bildtstar but not in those of Lady Rosetta, which indicated that chlorogenic acid may take part in black spot formation but was not essential for the discolouration. The results supported the hypothesis that black spot pigments were products of non-regulated reactions between nucleophilic amino acid residues in proteins and quinones, which were derived from endogenous substrates of polyphenol oxidase, indicating that black spot formation most probably occurred in disintegrated cells. Quantification of polyphenol oxidase (PPO), soluble protein and endogenous PPO substrates demonstrated that the content of free tyrosine was the predominant determinant for the biochemical potential for black spot synthesis (Stevens and Davelaar 1997).

Phytochemicals in Boiled/Cooked/Processed Potatoes

Volatile compounds in identified boiled potatoes of various cultivars included: methanol, ethanol, acetaldehyde, propanal, 2-methylbutanal, 2-methylpropanal, 2-methylbutanal, 3-methylbutanal, acetone, 2,3-butanedione, hydrogen sulphide, dimethyl disulphide, methyl mercaptan, ethyl mercaptan, methanethiol, diacetyl and ethanethiol (Self and Swain 1963). Volatile compounds produced by boiling potatoes were identified as hydrogen sulphide, acetaldehyde, methanethiol, acrolein, acetone, ethanethiol, dimethyl sulphide, isobutyraldehyde, n-butyraldehyde, isovaleraldehyde, butanal, 3-methylbutanal, 3-methyl-2-butanone and methyl isopropyl ketone, along with some unidentified components (Self et al. 1963). Thirty-five components were identified in potato essences and 20 in a potato granule essence (Nursten and Sheen 1974). 2-Methoxy-3-ethylpyrazine was present in potato volatiles and in potato sprout essence. Butanal and 3-methylbutanal was found only in cooked or

processed (granulated) but not raw potatoes. Volatile compounds identified in the headspace of boiled Russet Burbank potatoes included: 2-hexenal; heptanal; *c*4-heptenal; octanal; octenal, nonanal; 2-nonenal; decanal; 2,4-decadienal; 2,4-hetadienal; 2,4-nonadienal; 2,6-nonadienal; benzaldehyde; furfural; pentanol; hexanol; 2-octen-1-ol; 1-octen-3-ol; 1-octen-3-one; 2-undecanone; 3,5-octadien-2-one; 1,5-octadien-3-one; hexanoic acid; ethyl benzaldehyde; ethyl heptanoate; 2-methoxy-3-isopropylpyrazine; 2-methyl-3-isopropylpyrazine; 2-pentylfuran and pentyl oxirane (Josephson and Lindsay 1987). Dilute aqueous solutions of *c*4-heptenal exhibited boiled potato-like aromas, and at relatively high concentrations (greater than 0.7 ppb), the added *c*4-heptenal contributed to distinct staling-type flavour defects to both fresh and mashed potatoes. When added at levels between 0.1 and 0.4 ppb, *c*4-heptenal enhanced overall earthy, potato-like flavours in freshly boiled mashed potatoes, but these levels caused stale flavours in reconstituted dehydrated potatoes. Pentenal, 3-isopropyl-2-methoxypyrazine, hexanal, 2-heptanone, benzaldehyde, nonanal, naphthalene, decanal, copaene and pentadecane were identified in headspace concentrates of freshly boiled, earthy, musty-flavoured Russet Burbank potato tubers (Mazza and Pietrzak 1990).

The following compounds were identified in the steamed volatile oil of potatoes: 1-octen-3-ol; *trans*-2-octenal; *trans*-2-octenol; geraniol; 2-pentylfuran; phenylacetaldehyde; *trans*-2-nonenal; furfural; hexanal; acetaldehyde; isobutyraldehyde; heptanal; 2-heptenal; nonenal; 2,4-decadienal; benzaldehyde; methional; furfural; 2-methylbutanol; 3-methylbutanol; pentanol; 2-octen-1-ol; nerol, linalool and benzyl alcohol; terpineol; octenol; heptanone, 2-heptanone; 1-octen-3-one; 2-nonen-4-one; 2-decanone; methyl-2-hydroxybenzoate; methyl salicylate; biphenyl; naphthalene; 1-methylnaphthalene; pyridine; benzothiazole; and 3,5-dimethyl-1,2,4-trithiolane (Buttery et al. 1970). The difference thresholds of the six compounds in the reconstituted dehydrated mashed potato products varied from 0.05–3.1 ppm (Guadagni et al. 1971). Only

2-methoxy-3-ethylpyrazine (0.1–0.2 ppm) was effective in increasing the flavour level of all four brands of dehydrated potatoes; it also proved to be effective in increasing the potato flavour level of potato salad, dehydrated scalloped potatoes and potato soup. Potato salad stored at 3 °C for 1 week required at least 0.2 ppm of this compound to maintain its initial flavour difference from the control sample. Phenylacetaldehyde, oct-1-en-3-ol, methional and 2-methoxy-3-isopropylpyrazine were ineffective in increasing the flavour of reconstituted mashed potatoes. Volatile compounds that contribute to the flavour of steam-cooked mashed potatoes and reconstituted dehydrated potato granules were characterised and identified as pentenal; hexanal; 2-heptenal; octanal; 2,4-octadienal; octanol; furfuryl alcohol; *cis*-farnesol; mentadienol; 2,3-butadione; 2-butanone; 1-penten-3-one; 2-nonen-4-one; 3,5-octanedione; 2-methyl-3-octanone; 1,2-cyclohexandione; farnesyl acetone; geranylacetone; pentadecane; 2-pyridine methanol; 2-ethylfuran; 5-methylfural; dimethyl trisulphide; and dimethyl tetradisulphide (Salinas et al. 1994). The following volatiles were detected in raw and boiled potatoes: pentanal; hexanal; heptanal; 2-heptenal; 4-heptenal; 2-octenal; 2-nonenal; 2, 4-decadienal; 2,4-heptadienal; 2,4-nonadienal; 2,6-nonadienal; phenylacetaldehyde; 2-methylbutanol; ethanol, pentanol; benzyl alcohol; 1-penten-3-one; 1-methyl-2-pyrrolidone; acetic acid; propanoic acid; hexanoic acid; (*E*)-9-octadecene; 2-isobutyl-3-methoxypyrazine; 3-isobutyl-2-methoxypyrazine; 2-ethylfuran; and 2-pentylfuran (Petersen et al. 1998).

Mutti and Grosch (1999) found 45 odorants of boiled potatoes, of which 42 were identified. *trans*-4,5-Epoxy-(*E*)-2-decenal; methional; 2-acetyl-1-pyrroline; dimethyltrisulphide; 2,3-diethyl-5-methylpyrazine; vanillin; sotolon; decanal; (*E,E*)-2,4-nonadienal; (*E,E*)-2,4-decadienal, (*E*)- β -damascenone, furaneol, methanethiol, 3-isopropyl-2-methoxypyrazine and dimethyl sulphide were reported with a higher flavour dilution factor. Ulrich et al. (2000) reported the following basic odorants (component and sensory attribute) of boiled potato aroma: diacetyl (buttery, sweet, caramel); hexanal

(green); (*E*)-2-pentenal (roasty, rubber, unpleasant); 2-methylbutanol (unpleasant, sweat); 2-pentylfuran (unpleasant, green beans, cooked); methylpyrazine (nutty, strong); octan-2-one (mushroom, earthy); 2,6-dimethylpyrazine (nutty, warm); 2-methyl-5-isopropylpyrazine or 2-ethyl-6-methylpyrazine (nutty, warm, chemical); 3-ethyl-2,5-dimethylpyrazine (nutty, earthy, herbaceous); 2-ethyl-3,5-dimethylpyrazine (roasty, coffee-like); methional (cooked potato); pyrrole (nutty, roasty), 1-octanol; (*E,E*)-3,5-octadienone (nutty); (*E,E*)-2,6-nonadienal (fatty, cucumber); phenylacetaldehyde (flowery); 2,4-decadienal (fatty, unpleasant); unknown (unpleasant); and unknown (baked). Additional to these positive aroma compounds, an unknown substance, (*E*)-2-pentenal, 2-pentylfuran and at least four different dieneals ((*E,E*)-2,4-heptadienal, (*E,E*)-2,4-octadienal, (*E,Z*)-2,6-nonadienal, (*E,E*)-2,4-decadienal) were found to be off-flavour components. Eight compounds (pentanal, hexanal, nonanal, (*E*)-2-octenal, 2,4-heptadienal, (*E*)-2-nonenal, (*E,E*)-2,4-nonedienal and 2,4-decadienal) were deemed as potential contributors to boiled potato off-flavour, since these compounds could be detected during GC sniffing and increased in concentration during storage (Peterson et al. 1999). Off-flavours in boiled potatoes were found to be strongly correlated with the presence of 2-pentenal, 2-hexenal, 2-heptenal, 2-pentylfuran and 2-decenal (Blanda et al. 2010). In all, about 50 compounds were detected.

Mäder et al. (2009) found that processing potatoes to potato flakes markedly diminished the content of free phenolic compounds, total phenolics and glycoalkaloids, mainly due to peeling and leaching. The influence of thermal exposure was less significant. About 43 % of the initial phenolic acids (caffeic acid, gallic acid, ferulic acid, *p*-coumaric acid, *p*-hydroxybenzoic acid, protocatechuic acid, vanillic acid, catechin and three isomers of caffeoylquinic acid: chlorogenic, neochlorogenic and cryptochlorogenic acid) and 10 % of the glycoalkaloids (α -solanine and α -chaconine) remained after processing. Steam peeling had a higher influence on glycoalkaloid losses compared to that on phenolics. The highest

amounts of phenolic compounds and glycoalkaloids were found in peeling by-product. During processing, the amount of chlorogenic acid decreased, whereas the concentration of neochlorogenic acid increased due to isomerisation.

Phytochemicals in Dehydrated

Potatoes

2-Methylpropanal produced a characteristic wet fur flavour note, while 2- and 3-methylbutanal modified this flavour and contributed burnt flavour notes in explosion-puffed dehydrated potatoes (Sapers 1970). N-hexenal was also present. Acetone, which was also present in the headspace vapour of explosion-puffed dehydrated potatoes, was found as a major headspace component of fresh boiled potatoes. This compound and smaller amounts of 2- and 3-methylbutanal were produced in overcooked fresh potatoes which lacked the puffing off-flavour. Heights of peaks corresponding to 2-methylpropanal plus acetone, 2-methylbutanal plus 3-methylbutanal, hexanal and ethyl butyrate of explosion-puffed dehydrated potatoes were determined (Sapers et al. 1970). The intensity of the off-flavour was found to be associated with the heights of the 2-methylpropanal plus acetone and 2-methylbutanal plus 3-methylbutanal peaks. Peak heights of ten potato volatile components were associated with the intensity of a toasted off-flavour produced by the explosion puffing process (Sapers et al. 1971). Four of these and two additional minor components were found to have pyrazine-like aromas; two components had aromas characteristic of the thermal degradation of dry proline-glucose mixtures and two components had burnt aromas. 2-Methylpyrazine, 2,5-dimethylpyrazine, furfural, 5-methylfurfural, benzaldehyde and phenylacetaldehyde were identified, and an ethylmethylpyrazine, ethyldimethylpyrazine and trimethylpyrazine were tentatively identified. The results suggested that the toasted off-flavour was due to the presence of alkylpyrazines, compounds derived from proline, products of sugar pyrolysis and products of Strecker degradation reactions. Flavour volatiles associated with storage changes of potato flakes were benzaldehyde, hexanal, heptanal, 2-hexenal

and 2-pentylfuran (Sapers et al. 1972). Comparisons of dehydrated potato flakes drum dried at different rates and to different moisture contents indicated that overdrying reduced flake stability due to thermal damage during dehydration and to the low water activity of the overdried product (Sapers et al. 1974).

During the production of dehydrated cooked potato, the concentration of glycoalkaloids (α -chaconine and α -solanine) (TGA) and nitrates in processed potatoes decreased (Rytel 2012). TGA decreased most after peeling (30 %), blanching (28 %) and pre-drying (25 %). Nitrate content decreased significantly after blanching (21 %) and after pre-drying (18 %). During peeling of raw potatoes, the losses were about 20 % of the total content of both glycoalkaloids α -solanine and α -chaconine (factor=0.80) (Ostrý et al. 2010). Cooking of raw peeled potatoes until edible stage in salted water resulted in 20 % loss (factor=0.80). Combining both factors (for peeling and cooking) led to a combined loss of 36 % (factor=0.64) of total glycoalkaloids.

Phytochemicals in Baked Potatoes

Forty-two volatile compounds, mostly pyrazines and aliphatic aldehydes, were characterised in whole baked potatoes (Buttery et al. 1973). They stated the components most important to baked potato aroma included 2-ethyl-3,6-dimethylpyrazine, 3-methylmercaptopropanal (methional), deca-*trans,trans*-2,4-dienal and possibly 2-ethyl-3,5-dimethylpyrazine. Comparison of the volatile oils obtained from the baked potato skins and the potato pulp showed a considerably greater ratio of pyrazines to aldehydes in the skins indicating that the pyrazines were probably formed largely in the skins.

Pareless and Chang (1974) found that a combination of 2-isobutyl-3-methylpyrazine; 2,3-diethyl-5-methylpyrazine and 3,5-diethyl-2-methylpyrazine had an odour closer in character closer to baked potato than any other single compound. Eight other pyrazines were identified: 2-ethyl-3,5,6-trimethylpyrazine; isoamylmethylpyrazine; trimethylisobutylpyrazine; a diethylmethylpyrazine, two alkylpyrazines (Mw 164), a tetra-substituted alkylpyrazine (mw 178) and olefinic pyrazines (mw 148 and 178).

The following pyrazines, 2,3,5-trimethylpyrazine; 2,3,6-trimethyl-5-hydroxycyclopentapyrazine; 2,3-diethyl-5-methylpyrazine; 2,3-diethylpyrazine; 2,3-dimethyl-5-butylpyrazine; 2,3-dimethylpyrazine; 2,5-dimethyl-3-butylpyrazine; 2,5-dimethylpyrazine; 2,6-dimethyl-3-butylpyrazine; 2,6-dimethylpyrazine; 2-butyl-3-methylpyrazine; 2-butyl-6-methylpyrazine; 2-ethyl-3,5,6-trimethylpyrazine; 2-ethyl-3,5-dimethylpyrazine; 2-ethyl-3,6-dimethylpyrazine; 2-ethyl-3-methylpyrazine; 2-ethyl-5-methylpyrazine; 2-ethyl-6-methylpyrazine; 2-ethyl-6-propylpyrazine; 2-ethyl-6-vinylpyrazine; 2-isobutyl-2,5-dimethylpyrazine; 2-isobutyl-3-methylpyrazine; 2-isopropyl-3-methoxypyrazine; 2-methyl-6,7-dihydro-5*H*-cyclopentapyrazine; 3,5-diethyl-2-methylpyrazine; 3,5-dimethyl-6,7-dihydro-5*H*-cyclopentapyrazine; 3-butyl-2,5-dimethylpyrazine; 3-ethyl-2,5-dimethylpyrazine; 3-isoamyl-2,5-dimethylpyrazine; 3-isobutyl-2,5-dimethylpyrazine; 5,7-dimethyl-1,2,3,4,7,8-hexahydroquinoxaline; 5-butyl-2,3-dimethylpyrazine; 5-methyl-6,7-dihydro-5*H*-cyclopentapyrazine; ethylpyrazine; and methylpyrazine, and three thiazoles, 2,5-dimethyl-4-ethylthiazole; 2,5-dimethyl-4-butylthiazole and 2,5-dimethyl-4-methylthiazole, were identified in the volatile flavour of baked potatoes (Coleman and Ho 1980). Fourteen halogen compounds were identified in volatile flavour constituents of baked potatoes: 1,1,1-trichloroethane; tetrachloroethylene; trichloroacetic acid; 2-chloropropane; chloroform; 1-chloroheptane; 1,1-dichloroheptane; 1-chloro-2-methylbutane; *o*-chloroaniline; 2-chlorobiphenyl; 2-bromo-5-ethylnonane; *p*-chloroaniline; 1-iodooctadecane; and 1-chlorohexadecane (Ho and Coleman 1981).

A total of 228 compounds were identified in the volatiles of baked Idaho russet Burbank potatoes comprising aldehydes, alcohols, ketones, acids, hydrocarbons, esters, lactones, ethers, furans, halogenated compounds, pyrazines, oxazoles, thiazole, thiophenes and miscellaneous heterocycles (Coleman et al. 1981). The compound included aldehydes: (2-methylpropanal; 2-methyl-2-propanal; 3-methyl-1-butenal; 2-methyl-2-butenal; 3-methyl-2-butenal; pentanal; 2-pentenal; 4-methyl-2-phenyl-2-pentenenal; hexanal; 2-ethylhexanal; 5-methyl-2-phenylhexanal; 3-hexenal;

heptanal; nonanal; undecanal; *trans,trans*-2,4-decadienal; octadecanal; benzaldehyde; phenylacetaldehyde; ethylbenzaldehyde; 2,5-dimethylbenzaldehyde; methoxycinnamaldehyde; salicylaldehyde), alcohols: (methanol, ethanol; 2-butanol; 2-pentanol; 2-methyl-2-pentanol; 3-methyl-1-pentanol; 4-methyl-1-pentanol; 2,4-dimethyl-3-pentanol; 4-methyl-4-pentanol; 2-methyl-3-penten-2-ol; 2-methyl-1-penten-3-ol; heptanol; 3,6-dimethyl-3-octanol; 2-isobutyloctanol; 1-octen-3-ol; benzyl alcohol; dodecanol; hexadecanol; cyclohexanol; 2-ethyldecylcycloxyethanol; hexahydrofarnesol; trimethylbenzyl alcohol; 3-methoxy-4-isopropylbenzyl alcohol; and naphthol), ketones: (acetone; 1-phenyl-1,2-propanedione; 4-methyl-2-pentanone; 5-methoxy-2-pentanone; cyclopentanone; 2,5-dimethyl-1-cyclopentanone; 4-methyl-3-penten-2-one; 2,6-dimethyl-3-penten-2-one; hexanone; 2-acetyl-3,3-dimethylcyclohexanone; heptanone; 2-heptanone; 4-heptanone; 2-methyl-4-heptanone; 2-methyl-2-hepten-6-one; 3-octen-2-one; 4-decanone; and methyl acetophenone), acids: (acetic acid; propanoic acid; butanoic acid; pentanoic acid; hexanoic acid; heptanoic acid; 2-methylhexanoic acid; 2-methylpentanoic acid; 2-methylpropanoic acid; 3-methylbutanoic acid; 3-methylpentanoic acid; 4-methylpentanoic acid; 2-ketoadipic acid), esters: (1-methylpropyl acetate; 2-methylbutyl acetate; 2-methylbutyl pentanoate; allyl hexanoate; butyl acetate; diethyl phthalate; di-isobutyl phthalate; di-isobutyl isophthalate; ethyl acetate; hept-1-enyl-2-acetate; methyl-2-methylpropanoate; methyl hexanoate; methyl nonanoate; methyl octanoate; methyl pentanoate; pentyl acetate; phthalic anhydride), lactones: (4-pyridoxic lactone), hydrocarbons: (2-methyltetradecane; 2,6,10,14-tetramethylpentadecane; 5,7-dimethylhexadecane; 7,9-dimethylhexadecane; 2,6,11,15-tetramethylhexadecane; 2,4-dimethylheptane; 9-octylheptadecane; cyclodecane; 2,6,9-trimethylundecane; 2,6,10-trimethylundecane; 4,6-di-*n*-propyldodecane; 1-cyclopentyl-4-octyldodecane; 3,5,5-trimethyl-1-hexene; 2-ethyl-3-octene; 4-ethyl-3-octene; 1-octadiene; 1,4-dimethyl-4-vinylcyclohexene; diphenylmethane; 1-methylindan; 4,5,7-trimethylindan; limonene; α -pinene; 3-carene; benzene;

methyl-benzene (toluene); 1,2-dimethylbenzene; 1,3-dimethylbenzene; 1,4-dimethylbenzene; isopropylbenzene; trimethylbenzene; 3-ethylstyrene; *tert*-butylbenzene; *sec*-butylbenzene; 1,2,3,4-tetramethylbenzene; hexamethylbenzene; 1-methyl-4-ethylbenzene; nonylbenzene; biphenyl; diphenylmethane; 1,2-dimethynaphthalene; 1,3-dimethynaphthalene; 2,7-dimethynaphthalene; 1,3,8-trimethynaphthalene; 1,4,5-trimethynaphthalene; 1,4,6-trimethyl-1,2,3,4-tetrahydronaphthalene; 2-isopropyl-naphthalene; 3-methyleicosane; methylcyclopentane; γ -humulene; myrcene; cymene; *trans*, *trans*-farnesene; phellandrene), halogens: (chloroform; 1,1,1-trichloroethane; tetrachloroethylene; 1,1-dichloroheptane; 1-chloroheptane; 1-chlorobiphenyl; 2-chlorophenyl; 2-chloro-2-methylbutane; 1-chlorohexadecane; 2-chloropropane; *o*-chloroaniline; *p*-chloroaniline; trichloroacetic acid; 2-bromo-5-ethylnonane; 1-ioda-octadecane), pyrazines: (methylpyrazine; ethylpyrazine; 2,3,5-trimethylpyrazine; 2,3,5-trimethyl-5-hydroxy-cyclopentapyrazine; 2,3-diethyl-5-methylpyrazine; 2,3-diethylpyrazine; 2,3-dimethyl-5-butylpyrazine; 2,3-dimethylpyrazine; 2,5-dimethyl-3-butylpyrazine; 2,6-dimethyl-3-butylpyrazine; 2,5-dimethylpyrazine; 2,6-dimethylpyrazine; 2-butyl-3-methylpyrazine; 2-butyl-6-methylpyrazine; 2-ethyl-3,5,6-trimethylpyrazine; 2-ethyl-3,5-dimethylpyrazine; 2-ethyl-3,6-dimethylpyrazine; 2-ethyl-3-methylpyrazine; 2-ethyl-5-methylpyrazine; 2-ethyl-6-methylpyrazine; 2-ethyl-6-propylpyrazine; 2-ethyl-3,5,6-trimethylpyrazine; 2-ethyl-6-propylpyrazine; 2-ethyl-6-vinylpyrazine; 2-isobutyl-3-methylpyrazine; 3,5-diethyl-2-methylpyrazine; 2-methyl-6,7-dihydro-5*H*-cyclopentapyrazine; 3,5-dimethyl-6,7-dihydro-5*H*-cyclopentapyrazine; 5-methyl-6,7-dihydro-5*H*-cyclopentapyrazine; 5-butyl-2,3-dimethylpyrazine; 3-butyl-2,5-dimethylpyrazine; 3-ethyl-2,5-dimethylpyrazine; 2,3,6-trimethyl-5-hydroxy-cyclopentapyrazine; 5,7-dimethyl-1,2,3,4,7,8-hexahydroquinoxaline), pyridines: (2-aminopyridine; 2-acetylpyridine), pyrroles: (2-acetylpyrrole; 2-acetyl-1-pyrroline; *N*-methyl-2-formylpyrrole), furans: (2-furaldehyde; 2-pentylfuran; 2-acetylfuran; 2-propionylfuran; 2-methylfurfural; furfural; *trans*-2-(2-pentenyl)furan; methyl furoate; 2,5-dimethyltetrahydrofu-

ran; 2-methyltetrahydrofuran-3-one; 2-methyl-3-(2*H*)-furanone), ethers: (methyl ether; ethyl isopropyl ether; ethyl pentyl ether; ethyl nonyl ether; diethylene glycol diethyl ether; 1-ethoxy-1-propoxyethane; 1,1-diethoxyisopentane), thiazoles: (2,5-dimethyl-4-ethylthiazole; 2,5-dimethyl-4-butylthiazole; 2,5-diethyl-4-methylthiazole), thiophenes: (thiophene; 2-formylthiophene; 2-butyl-6-ethylthiophene), oxazoles: (2,4,5-trimethyloxazole; 5-acetyl-2,4-dimethyloxazole), sulphur compounds: (2-ethylhexyl mercaptan), nitrogen-containing compounds: (2-isopropylbenzimidazole; diethylformamide; diethylacetamide; diphenylamine; cyanobenzene; 2-amino-4-nitrotoluene; 2-aminopentane) and miscellaneous heterocycles: (2-propyl-1,3-dioxolane; 2,4,6-trimethyl-1,3,5-trioxane). The following compounds were deemed most important to baked potato aroma: 2-ethyl-3-6-dimethylpyrazine; methional, *trans*,*trans*-2,4-decadienal; and possibly 2-ethyl-3-5-dimethylpyrazine (Coleman et al. 1981).

The following flavour components were identified in the volatiles of baked potatoes of four cultivars: 2-methyl-2-butenal; pentanal; pentenal; 2-pentenal; hexanal; 2-hexenal; heptanal; 2-heptenal; octanal; 2-octenal; nonanal; 2-nonenal; 2,4-heptadienal; 2,4-nonadienal; benzaldehyde; phenylacetaldehyde; methional; furfural; 2-methylbutanol; 3-methylbutanol; hexanol; 2-ethyl-hexanol; 3-hexen-1-ol; 1-octen-3-ol; linalool; 2,3-pentadione; 2-heptanone; 6-methyl-5-hepten-2-one; 4-octen-3-one; 2,3-octadione; methyl-2-methylbutanoate; methylbutanoate; 2,2,4,6,6-pentamethylheptane; copaene; limonene; α -pinene; β -pinene; 3-carene; benzene; toluene; ethylbenzene; 1,2-dimethylbenzene; 1,3-dimethylbenzene; 1,4-dimethylbenzene; trimethylbenzene; propylbenzene; 2-methylvinylbenzene; methylpropylbenzene; naphthalene; myrcene; cymene; 2,5-dimethylpyrazine; 2,6-dimethylpyrazine; 2-isopropyl-3-methoxypyrazine; 3-ethyl-2,5-dimethylpyrazine; methylpyrazine; 2-ethylfuran; 2-pentylfuran; 2-methyl-3(2*H*)-furanone; methyl-*N*-pentyl disulphide; dimethyl disulphide; dimethyl trisulphide; and dimethyl tetrasulphide (Oruna-concha et al. 2001). Eighty

flavour components were identified in eight potato cultivars baked in microwave oven: hexanal; 2-heptenal; nonanal; decanal; undecanal; 2-undecanal; 2-dodecanal; hexadecanal; 2,4-decadienal; 2,4-heptadienal; 2,4-nonadienal; benzaldehyde; phenylacetaldehyde; methional; 2-furfural; 5-methylfurfural; 5-methyl-2-furfural; 5-methyl-2-thiophenecarboxaldehyde; 3-methylbutanol; 1-octen-3-ol; hexadecanol; 2-methoxyphenol; eugenol; 4-vinyl-2-methoxyphenol; 2-methoxy-4-vinylphenol; 3-ethylcyclopentanone; 2-pentadecanone; 3,5,5-trimethyl-3-cyclohexene-1-one; 2,3-octadione; 3,5-octadien-2-one; solavetivone; methyl hexadecanoate; methyl octadecanoate; methyl tetradecanoate; octadecyl acetate; cycloheptane; undecane; limonene; ethylbenzene; propylbenzene; 2-methylnaphthalene; 2,3,5-trimethyl-6-(3-methylbutyl)pyrazine; 2,3-diethyl-5-methylpyrazine; 2,5-dimethyl-3-(2-methylpropyl)pyrazine; 2,5-dimethyl-3-(3-methylbutyl)pyrazine; 2,5-dimethyl-3-propenylpyrazine; 2,5-dimethylpyrazine; 2,6-dimethyl-3-(2-methylbutyl)pyrazine; 2,6-dimethylpyrazine; 2-ethenyl-5-methylpyrazine; 2-ethenyl-6-methylpyrazine; 2-ethyl-3,6-dimethylpyrazine; 2-ethyl-3-methylpyrazine; 2-ethyl-5-methylpyrazine; 2-ethyl-6-methylpyrazine; 2-isopropyl-3-methoxypyrazine; 2-methyl-5-propenylpyrazine; 3,5-diethyl-2-methylpyrazine; 3,5-diethyl-2-(2-methylpropyl)pyrazine; 3-ethyl-2,5-dimethylpyrazine; ethylpyrazine; methylpyrazine; trimethylpyrazine; pyridine; 2-acetylpyrrole; 2-acetyl-1-pyrroline; 1-methyl-1(*H*)-pyrrole; 1-(2-furanylmethyl)-1(*H*)-pyrrole; 2-pentylfuran; 2,5-dihydrofuran; methylpropyl disulphide; methyl-*N*-pentyl disulphide; dimethyl disulphide; dimethyl trisulphide; dimethyl tetrasulphide; ethyl pentyl disulphide; benzyl methyl sulphide; benzyl methyl disulphide; and dipentyl disulphide (Oruna-Concha et al. 2002a). Quantitative and qualitative differences were observed between isolates from flesh and skins and among the four cultivars grown at different sites. Lipid and sugar degradation and/or the Maillard reaction were the main origins of volatiles in flesh. The two main sources of flavour compounds (regardless of cooking procedure)

were lipid degradation and the Maillard reaction and/or sugar degradation (Oruna-Concha et al. 2002b). The ratio (yield derived from lipid)/(yield derived from Maillard reaction and/or sugar) decreased from 8.5–9.1 (boiling) to 2.7–3.4 (microwave baking) and to 0.4–1.1 (conventional baking).

The volatile flavour components of baked potatoes were identified as: decanal; 3-methylbutanal; methylpropanal; 2-methylpropanal; 2-methylbutanal; 3-methylbutanal; methional; pentanal; hexanal; heptanal; 2-heptenal; octanal; nonanal; 2-nonenal; undecanal; dodecanal; benzaldehyde; phenylacetaldehyde; 2-furfural; β -damascenone; 2-methylbutanol; 3-methylbutanol; hexanol; 1-octen-3-ol; linalool; butanedione; 2,3-pentadione; butanone; 3-hexanone; 2-heptanone; 5-methyl-5-hepten-2-one; geranyl acetone; solavetivone; ethyl acetate; methylbutanoate; copaene; α -aromadendrene; guaiane; limonene, α -pinene; 3-carene, benzene, toluene; ethyl benzene; 1,2-dimethylbenzene; 1,3-dimethylbenzene; 1,4-dimethylbenzene; styrene; naphthalene; methylcyclopentane; myrcene; ocimene; cymene; terpinolene; phellandrene; 2,5-diethyl-5-pyrazine; 2,5-dimethylpyrazine; 2-ethyl-3,6-dimethylpyrazine; 2-ethyl-3-methylpyrazine; 2-ethyl-5-methylpyrazine; 2-ethyl-6-methylpyrazine; 3,5-diethyl-2-methylpyrazine; 3,5-dimethyl-2-(2-methylpropyl)pyrazine; 2-ethyl-2,5-dimethylpyrazine; 2-isopropyl-3-methoxypyrazine; 2-isobutyl-3-ethoxypyrazine; 3-isopropyl-2-methoxypyrazine; ethylpyrazine; methylpyrazine; pyridine; 1-methyl-1(*H*)-pyrrole; 2-ethylfuran; 2-pentylfuran; 2-methylfuran; dimethyl disulphide; dimethyl trisulphide; and dimethyl tetrasulphide (Duckman et al. 2001, 2002). Lipid degradation and the Maillard reaction were the main sources of flavour compounds, accounting for 22–69 % and 28–77 %, respectively, of the total yields in baked potatoes (Duckham et al. 2001). Various sulphur compounds, methoxypyrazines and terpenes were also identified at lower levels. Compounds contributing most to baked aroma (relative aroma impact value (RAV) > 10,000 in at least one cultivar) were 2-isobutyl-3-methoxypyrazine, 2-isopropyl-3-methoxypyrazine, β -damascenone, dimethyl trisulphide, decanal and 3-methylbutanal. Of the compounds monitored,

those most likely having the greatest flavour impact in baked potatoes were 2-isopropyl-3-methoxy-pyrazine, 2-isobutyl-3-methoxy-pyrazine, dimethyl trisulphide, decanal and 3-methylbutanal, with methylpropanal, 2-methylbutanal, methional and nonanal also being probable important contributors to flavour (Duckham et al. 2002).

Phytochemicals in Potato Chips

The following compounds were identified as contributing to potato chip flavour, namely, alcohols (2-butanol; 3-methyl-1-butanol; 1-pentanol; 2-furfuryl alcohol; α -terpineol), aldehydes (2-methylpropanal; 2-methylbutanal; 3-methylbutanal; 2-isopropyl-2-butenal; 4-methyl-2-pentenal; *trans*-2-hexenal; 4-methyl-2-hexenal; *trans*-2,*trans*-4-octadienal; *trans*-2-nonenal; *trans*-2,*trans*-4-nonadienal; benzaldehyde; 2-phenyl-2-butenal; 4-methyl-2-phenyl-2-pentenal; 5-methyl-2-phenylhexanal; 2-octenal, ethanal (acetaldehyde); 2-phenylacetaldehyde; hexanal; pentanal; 2-heptenal; 2-octenal; propenal; *n*-butanal; 2-pentenal; 2-hexenal; *n*-heptanal; 2-heptenal; deca-2,4-dienal), ketones (2,3-butanedione; 2-propanone; 2-pentanone), furans (2-butylfuran; 2-pentylfuran; 2-hexylfuran; furfural; 5-methylfurfural; 2-methyldihydro-3(2H)-furanone; 2-acetylfuran; furfuryl alcohol), hydrocarbons (1-decyne), ketones (2-butanone; 2,3-butanedione; *trans*-3-penten-2-one; 2,3-pentanedione; 5-methyl-2,3-hexanedione; *trans*-2-nonen-4-one; 2-decanone; acetophenone), pyrazines (2-methylpyrazine; 2,3-dimethylpyrazine; 2,5-dimethylpyrazine; 2,6-dimethylpyrazine; 2-ethylpyrazine; 2-ethyl-3-methylpyrazine; 2-ethyl-5-methylpyrazine; 2-ethyl-6-methylpyrazine; 2,3,5-trimethylpyrazine; 2-methyl-5-vinylpyrazine; 2-ethyl, 3,6-dimethylpyrazine; 2-ethyl-3-5-dimethylpyrazine; 2,6-diethylpyrazine; 2-isobutyl-3-methylpyrazine; 2,3-diethyl-5-methylpyrazine; 2-isobutyl-3,6-dimethylpyrazine; 2-methyl-6-vinylpyrazine; 2,5-dimethyl-3-vinylpyrazine; 2,5-dimethyl-6-isopropylpyrazine; 2-isoamyl-5-methylpyrazine; methylethylisobutylpyrazine; 2-isobutenyl-3-methylpyrazine; 2-isoamyl-3,6-dimethylpyrazine; isobutenyldimethylpyrazine), pyridines and pyrroles (pyridine; 2-acetylpyridine; 2-acetylpyrrole) and

sulphur compounds ((methylthio)acetaldehyde and methional (3-methylmercaptopropanal)) (Deck and Chang 1965; Mookherjee et al. 1965; Dornseifer and Powers 1965; Buttery et al. 1971; Buttery and Ling 1972; Guadagni et al. 1972; Buttery 1973; Maga 1994; Koehler et al. 1971). Deck and Chang (1965) identified 2,5-dimethylpyrazine in potato chips imparting a typical raw earthy potato flavour at a concentration of approximately 10 ppm. Dornseifer and Powers (1965) reported changes in volatile carbonyls of potato chips during storage; they identified 2,3-butanedione, 2-propanone, ethanal, propenal, *n*-butanal, 2-pentenal, 2-hexenal, *n*-heptanal and 2-heptenal. Mookherjee et al. (1965) identified 18 monocarbonyl compounds in fresh potato chips and 19 compounds in stale but not rancid sample. Among saturated aldehydes, the largest increase during storage was in hexanal and next in pentanal; among the 2-alkanones the important increase was in 2-pentanone and next in 2-propanone, and among the 2-enals the largest increase was in 2-heptenal and 2-octenal. Only one 2,4-dienal, viz. 2,4-decadienal, was found in both fresh and stale potato chips; 4-decadienal which had a characteristic deep-fried flavour was greatly reduced during storage. Of the 18 pyrazine and pyridine compounds identified, 2-ethyl-3,6-dimethylpyrazine was found to be a major contributor to the odour intensity of potato chips (Buttery et al. 1971). Of the 46 compounds identified in non-basic steam volatile components of potato chips, methional, 3-methylbutanal, phenylacetaldehyde and 2,4-decadienal were determined to be important determinants of flavour (Buttery and Ling 1972). Koehler et al. (1971) found 2-ethyl-3,6-dimethylpyrazine to be a significant contributor to potato chip aroma. Guadagni et al. (1972) found 3-methylmercaptopropanal (methional) to be probably one of the most important contributors to potato chip aroma; other compounds that may contribute in varying degrees include deca-2,4-dienal, 2-ethyl-3,6-dimethylpyrazine, 2-acetyl-1,4,5,6-tetrahydropyridine, 2,6-diethylpyrazine, 2-octenal and 2-phenylacetaldehyde. The following volatile compounds were identified from

potato chips: heptane; nonane; decane; undecane; tetradecane; 2-methyl-1-butene; limonene; 3-*p*-menthene; α -terpinene; ethylbenzene; 1,2,4-trimethylbenzene; 1-ethyl-3,5-dimethylbenzene; benzaldehyde; phenylacetaldehyde; 2,6-di-*t*-butyl-4-hydroxytoluene; ethanol; acetaldehyde; butanal; pentanal; hexanal; heptanal; 2-heptenal; 2-octenal; hepta-2,4-dienal; deca-2,4-dienal; cyclopentanone; pentanoic acid; hexanoic acid; heptanoic acid; octanoic acid; decanoic acid; 2-methylpropanoic acid; 3-methylbutanoic acid; propyl acetate; butyl acetate; diphenyl ether; dimethyl disulphide; benzylthiobenzoate; 2-ethylpyrazine; 2,5-dimethylpyrazine; 2,6-dimethylpyrazine; 2-ethyl-5-methylpyrazine; 2,5-diethylpyrazine; 2,3,5-trimethylpyrazine; 2-ethyl-3,6-dimethylpyrazine; pyridine; 2-acetylfuran; and furfural (Deck et al. 1973).

Unusual aldehydes, 4-methylpent-2-enal; 4-methylhex-2-enal; 2-isopropylbut-2-enal; 2-methylmercaptomethylbut-2-enal; 2-methylmercaptomethyl-4-methylpent-2-enal; 2-phenylbut-2-enal; 2-phenyl-4-methylpent-2-enal; and 2-phenyl-5-methylhex-2-enal, were identified in potato chips, probably formed during frying by aldol-type condensation (Buttery 1973). Other compounds characterised included 2-methylhexa-4,5-dione; acetophenone; hepta-*trans,trans*-2-4-dienal; octa-*trans-trans*-2-4-dienal; nona-2,4-dienal; acetylbenzene; 2-isopropyl-2-butenal; 2-phenyl-2-butenal; 4-methyl-2-pentenal; 4-methyl-2-hexenal; 5-methyl-2-hexenal; 2-phenyl-4-methyl-2-pentenal; and 2-phenyl-5-methyl-2-hexenal (Buttery 1973). Taste panel described odour of potato chips as strong potato, baked potato and earthy potato (Maga 1994).

A large number of heterocyclic compounds were identified in baked Idaho Russet Burbank potatoes (Ho and Coleman 1980). This included furans (2-methylketotetrahydrofuran; methylfuroate; 5-methyl-2-furaldehyde; furfural; 2,5-dimethyl-tetrahydrofuran; *trans*-2-(2-pentyl)-furan; 2-acetyl furan; 2-pentyl furan; 2-propionylfuran), oxazoles (2,4,5-trimethyloxazole; 5-acetyl-2,4-dimethyloxazole), thiophenes (2-formylthiophene; 2-butyl-5-ethylthiophene) and pyrroles (2-acetylpyrrole; N-methyl-2-formylpyrrole; 1-dioxolane; and 1-trioxane). It

was noted that heterocyclic compounds with formyl or acetyl substituents had aromas with nutty characteristics.

The following nitrogen-containing compounds were identified in potato chips head space by comprehensive two-dimensional gas chromatography–time-of-flight mass spectrometry (GC \times GC–TOFM): pyrazine; pyrrole; pyridine; 1-ethyl-1*H*-pyrrole; 2-methylpyridine; 2-methylpyrazine; 2-methyl-1*H*-pyrrole; 3-methyl-1*H*-pyrrole; 3-methylpyridine; 2,6-dimethyl pyridine; 2-ethylpyridine; 2,5-dimethylpyrazine; 2,6-dimethylpyrazine; ethyl pyrazine; 2-ethyl-1*H*-pyrrole; 2,3-dimethylpyrazine; ethenylpyrazine; 1-butyl-1*H*-pyrrole; 2-pyridinecarboxaldehyde; 3-ethylpyridine; 2-ethyl-6-methylpyrazine; 2-ethyl-5-methylpyrazine; 2,3,5-trimethylpyrazine; 2-ethyl-3-methylpyrazine; 2-(*n*-propyl)-pyrazine; 1*H*-pyrrole-2-carboxaldehyde; 2-carboxaldehyde; 1-methyl-1*H*-pyrrole; 2-ethenyl-6-methylpyrazine; 2-ethenyl-5-methylpyrazine; *N*-acetyl-4(*H*)-pyridine; acetylpyridine; acetylpyrazine; 1-pentyl-1*H*-pyrrole; 1-methyl-2-pyrrolidinone; 2-acetylpyrrole; 2-ethyl-3,5-dimethylpyrazine; 2-ethyl-3,6-dimethylpyrazine; 2-pyrrolidinone; 3-acetyl-3-methylpyrazine; tetramethylpyrazine; 2-methyl-5-(1-propenyl)-(*E*)-pyrazine; 1-pyrrolidinecarboxaldehyde; 2-acetyl-3-methylpyrazine; (1-methylethenyl)-pyrazine; 2-acetyl-3-methylpyrazine; 2-isobutyl-3-methylpyrazine; 1-(2-pyridynyl)-1-propane; 2,3-diethyl-5-methylpyrazine; 3,5-diethyl-2-methylpyrazine; 5-methyl-5*H*-cyclopenta[b]pyrazine; 3,5-diethyl-2-methylpyrazine; 2-butyl-3-methylpyrazine; 3,5-dimethyl-2-isobutylpyrazine; 2-pyridinecarboxaldehyde; 2-methyl-5-(1-propenyl)-pyrazine; 1-acetyl-1,2,3,4-tetrahydropyridine; 5,6,7,8-tetrahydroquinoxaline; and 2-butyl-3-methylpyrazine (Lojzova et al. 2009).

Chemical composition (g/100 g chips) of fresh potato chips fried in mid-oleic sunflower oil was found to contain: moisture 1.96 g, fat 39.19 g, fatty acid (g/100 g oil from chips), myristic acid (C14:0) 0.35 g, palmitic acid (C16:0) 4.62 g, palmitoleic acid (C16:1n7) 0.08, stearic acid (C18:0) 4.47 g, oleic acid (C18:1n9) 57.73 g, linoleic acid (C18:2n6c) 31.02 g, α -linolenic acid (C18:3n3) 0.31 g, arachidic acid (C20:0) 0.29 g, *cis*-11-eicosenoic acid (C20:1n9) 0.23 g and behenic

acid (C22:0) 0.91 g (Lee and Pangoli 2013). Twenty-one flavour volatiles were isolated from potato chips fried in mid-oleic sunflower oil, but only 16 compounds were positively identified: hexanal; *trans*-2-pentenal; heptanal; *trans*-2-hexanal; octanal; *trans*-2-octenal; *trans*-2-heptenal; nonanal; 2-furaldehyde; decanal; benzaldehyde; *trans*-2-nonenal; *trans*-2-decenal; tetradecanal; hexadecanal; and *trans,trans*-2,4-decadienal (Lee and Pangoli 2013).

Phytochemicals in Crisped/French Fried Potatoes

Twenty-four alkyloxazole compounds were identified in the volatiles from French fried potatoes: trimethyl oxazole; 2 ethyl-4,5-dimethyl oxazole; 5-ethyl-2,4-dimethyloxazole; 2-ethyl-4-methyl-5-propyloxazole; 2,4-dimethyl-5-propyloxazole; 4-ethyl-2-methyloxazole; 4,5-dimethyl-2-isopropyloxazole; 4-n-butyl-2,5-imethyloxazole; 2-methyl-4-butyloxazole; 2-hexyl-4,5-dimethyloxazole; 2-butyl-4,5-dimethyloxazole; 2-butyl-4-propyl-5-methyloxazole; 2-pentyl-4-methyl-5-ethyloxazole; 2-hexyl-4-methyl-5-ethyloxazole; 2-methyl-4-ethyl-5-propyloxazole; 2-pentyl-4,5-dimethyloxazole; 2-butyl-4,5-diethyloxazole; 2,4-dimethyl-5-butyloxazole; 2-methyl-4-pentyloxazole; 2-pentyl-4-methyloxazole; 2,4,5-trimethyloxazole; 2-isopropyl-4,5-dimethyloxazole; 5-acetyl-2,4-dimethyloxazole; and 2-methyl-4-pentyloxazole (Carlin et al. 1986). Two new S-containing compounds were isolated and identified from French fried potatoes as 3-(methylthio)butanal and 3-(methylthio)heptanal (Carlin et al. 1990).

Among the 48 odour compounds identified in French fries, potent odorant found from Maillard reaction products included methional; furaneol; sotolone; 2-ethyl-3,5-dimethylpyrazine; 2,3-diethyl-5-methylpyrazine; 3-ethyl-2,5-dimethylpyrazine; dimethyltrisulphide; and 3-methylbutanal and from lipid oxidation products were (*E,E*)-2,4-decadienal; *trans*-4,5-epoxy-(*E*)-2-decenal; (*Z*)-2-nonenal; (*E*)-2-nonenal; and (*E,Z*)-2,4-decadienal (Wagner and Grosch 1997). Methional; 2-ethyl-3, 5-dimethylpyrazine; 2,3-diethyl-5-methylpyrazine; (*E,E*)-2,4-decadienal; 4-hydroxy-2,5-dimethyl-3(2H)-furanone; methanethiol; dimethyltrisulphide;

3-methylbutanal; and 2,3-butanedione (IX) showed high factors of dilution. The concentration of the most potent odorants found in French fries and their attributes were 2,3-diethyl-5-methylpyrazine 400 µg/kg with an earthy attribute; (*E,E*)-2,4-decadienal 900 µg/kg with deep-fried, fatty note; methional 1 µg/kg boiled potato attribute; furaneol 125 µg/kg sweet caramel; and 3-methylbutanal 30 µg/kg with a malty attribute. The deep-fried note (caused by (*E,E*)-2,4-decadienal) predominated when the French fries were nasally evaluated, whereas the deep-fried and boiled potato-like smells (caused by methional) were mainly perceived in the retronasal test. Twenty-one compounds were identified as potent odorants of French fries prepared in palm oil (PO): 2-ethyl-3,5-dimethylpyrazine; 3-ethyl-2,5-dimethylpyrazine; 2,3-diethyl-5-methylpyrazine; 2-ethenyl-3-ethyl-5-methylpyrazine; 3-isobutyl-2-methoxypyrazine; 1-octen-3-one; (*Z*)-2-nonenal; (*E*)-2-nonenal; (*E,E*)-2,4-nonadienal; (*E,Z*)-2,4-decadienal; (*E,E*)-2,4-decadienal; *trans*-4,5-epoxy-(*E*)-2-decenal; 4-hydroxy-2,5-dimethyl-3(2H)-furanone; 3-hydroxy-4,5-dimethyl-2(5H)-furanone; methylpropanal; 2-methylbutanal; 3-methylbutanal; 2,3-butanedione; methional; methanethiol; dimethyltrisulphide; 2-ethyl-3,5-dimethylpyrazine; 3-ethyl-2,5-dimethylpyrazine; 2,3-diethyl-5-methylpyrazine; 2-ethenyl-3-ethyl-5-methylpyrazine; 3-isobutyl-2-methoxypyrazine; 1-ccten-3-one; (*Z*)-2-nonenal; (*E*)-2-nonenal; (*E,E*)-2,4-nonadienal; (*E,Z*)-2,4-decadienal; (*E,E*)-2,4-decadienal; *trans*-4,5-epoxy-(*E*)-2-decenal; 4-hydroxy-2,5-dimethyl-3(2H)-furanone; 3-hydroxy-4,5-dimethyl-2(5H)-furanone; methylpropanal; 2-methylbutanal; 3-methylbutanal; 2,3-butanedione; methional; methanethiol; and dimethyltrisulphide (Wagner and Grosch 1998). In addition to these 21 compounds, γ-octalactone, γ-nonalactone, γ-decalactone and δ-decalactone were found in French fries prepared in coconut fat. γ-Octalactone was identified as a major contributor to this note.

Relative amounts (in gas chromatographic (GC) peak area units) of selected flavour compounds formed in potato slices fried in palmolein or silicone fluid were reported, respectively, as: methyl propanal (649.8, 548.9), 3-methylbutanal

(941.6, 948.5), 2-methylbutanal (1227.2, 1156.2), phenylacetaldehyde (50.7, 57.3), methional (3.6, 2.9), dimethyl disulphide (196.5, 167.8), dimethyl trisulphide (13, 20.5), pyrazine (1.1, 0.6), methylpyrazine (53.7, 19.1), 2,5(6)-dimethylpyrazine (74.8, 28), ethylpyrazine (22.9, 10.4), 2,3-dimethylpyrazine (9.0, 4.0), vinylpyrazine (3.8, 2.1), 2-ethyl-6-methylpyrazine (16.9, 6.2), 2-ethyl-5(3)-methylpyrazine (54.8, 24.2), 6-vinyl-6-methylpyrazine (9.2, 5.5), 3-ethyl-2,5-dimethylpyrazine (32.4, 15.5), hexanal (40.1, 62.2), (*E,Z*)-2,4-decadienal (40.2, 0.4) and (*E,E*)-2,4-decadienal (10.52, 0.0) (Martin and Ames 2001). Levels of Strecker aldehydes and sulphides in chips fried in the two media were not significantly different, but levels of pyrazines were significantly higher in palmolein-fried chips. Amounts of 2,4-decadienal were also significantly higher in palmolein-fried chips, but there was no significant difference in hexanal levels between the samples.

A total of 31 compounds including hexanal were identified in oxidised potato crisps that resulted mainly from the degradation/rearrangement of lipids and carbohydrates (Sanches-Silva et al. 2005). Tajner-Czopek et al. (2014) found that blue-fleshed potatoes, Vitelotte variety and red-fleshed Highland Burgundy Red variety could be used for French fries processing due to their low content of TGA (total glycoalkaloids α -solanine and α -chaconine) in unpeeled and peeled potatoes. However, blue-fleshed Blue Congo variety should not be used for French fries processing because of high TGA in unpeeled and peeled potatoes. The peeling of coloured-fleshed potatoes decreased TGA content (α -solanine and α -chaconine) by about 50 %, cutting process by about 53 % and blanching by about 58 % compared with the raw material. The highest decrease in TGA content was caused by the frying process.

Skatole, indole and *p*-cresol were identified as the main volatile components in off-flavoured French fries (Whitfield et al. 1982). It was suggested that *p*-cresol and skatole, the main faecal off odour compounds, might be formed in potatoes by a bacterial degradation of the amino acids tyrosine and tryptophan.

Acrylamide in Potatoes

Mottram et al. (2002) reported acrylamide to be generated from food components during heat treatment as a result of the Maillard reaction between amino acids and reducing sugars. They found that asparagine, a major amino acid in potatoes and cereals, was a crucial participant in the production of acrylamide by this pathway. Acrylamide levels in the products were significantly reduced if tubers were preconditioned before being placed in storage at 2 °C. Acrylamide, a chemical that formed when certain starchy foods were cooked or processed, had been shown to cause cancer in animals (FSANZ 2014; USFDA 2008; Beth and Bussan 2013). Acrylamide is typically found in plant-based foods cooked with high heat (e.g. frying, roasting and baking) not raw plant-based foods or foods cooked by steaming or boiling. Some foods are larger sources of acrylamide in the diet, including certain potato products (especially French fries and potato chips), coffee and cereal-based products (such as breakfast cereal, cookies, sweet biscuits and toast bread) which are all part of a regular diet. Beth and Bussan (2013) conducted a comprehensive review on acrylamide in processed potato products and health concerns covering animal and epidemiological research studies and mitigation strategic studies conducted to date.

Glucose and fructose concentrations in the tubers were significantly and positively correlated with subsequent acrylamide formation in the products (Silva and Simon 2005). Glucose, fructose, sucrose and asparagine concentrations in tubers increased upon storage at 2 °C. Tuber sucrose and asparagine concentrations did not have an effect on acrylamide levels. Studies by Ohara-Takada et al. (2005) suggested that the content of reducing sugars in potato tubers determined the degree of acrylamide formation in chips after frying. There was strong correlation between the reducing sugar content and acrylamide level, $R^2=0.873$ for fructose and $R^2=0.836$ for glucose. The sucrose content had less correlation with the acrylamide content. The chip colour, as evaluated by L^* (lightness), was correlated well with the acrylamide content. Matsuura-Endo

et al. (2006) found that at storage temperatures $<8^{\circ}\text{C}$ the contents of reducing sugars increased markedly in all potato cultivars, with similar increases in the acrylamide level and dark brown chip colour. The contents of reducing sugars correlated well with the acrylamide level when the fructose/asparagine molar ratio in the tubers was <2 . When the fructose/asparagine ratio was >2 by low-temperature storage, the asparagine content, rather than the reducing sugar content, was found to be the limiting factor for acrylamide formation. High correlations were observed between the acrylamide content in potato chips and glucose and fructose contents in the tubers indicating that the limiting factor for acrylamide formation in potato chips was reducing sugars, not asparagine content in the tubers (Yoshida et al. 2005).

Acrylamide is formed through the Maillard reaction during high-temperature cooking, such as frying, roasting or baking, and the main precursors are free asparagines as in wheat and reducing sugars as in potatoes (Muttucumaru et al. 2008). However, in potatoes, when sugar levels are limiting, competition between asparagine and the other amino acids for participation in the Maillard reaction determines acrylamide formation. Improvement in parameters such as (1) potato variety, (2) potato storage temperature, (3) process control (thermal input, pre-processing), (4) final preparation and (5) colour had all contributed to a significant overall reduction in the average acrylamide content in French fries and potato crisps (termed 'chips' in the USA) (Foot et al. 2007). The use of asparaginase offered potentially significant reduction in certain prefabricated potato products. Halford et al. (2012) reported that glucose and fructose showed the best correlations with acrylamide formation in both crisps and heated flour produced from nine varieties of potatoes grown commercially in the UK in 2009. However, free asparagine and total free amino acid concentrations also correlated with acrylamide formation in French fry varieties. Acrylamide formation, measured in heated potato flour, correlated with glucose and fructose concentration (Muttucumaru et al. 2014b). In French fry potato varieties, containing

higher concentrations of sugars, acrylamide formation also correlated with free asparagine concentration, demonstrating the complex relationship between precursor concentration and acrylamide-forming potential in potato. Storage of the potatoes for 6 months at 9°C had a significant, variety-dependent impact on sugar and amino acid concentrations and acrylamide-forming potential. Asparagine the predominant free amino acid in potato tubers was shown not to play an important role in the transport of nitrogen from leaf to tuber in potato and that the high concentrations of free asparagine that accumulated in potato tubers arose from synthesis in situ (Muttucumaru et al. 2014a). The study demonstrated that glutamine, glutamate and serine were the major transport amino acids from leaf to tubers in potato with alanine, aspartate, GABA, glycine, phenylalanine, proline, threonine and valine also playing a role.

Ye et al. (2011) found that microwaving treatment of potato chips could form more acrylamide from methylglyoxal, the main α -dicarbonyl, compared with frying method. Microwaving treatment promoted the formation of methylglyoxal compared with frying treatment at 160 and 180°C in potato chips. There was a significant correlation between methylglyoxal and acrylamide in potato chips, thus confirming the important role of dicarbonyls in the formation of acrylamide in potato chips. Miao et al. (2014) found that formation of acrylamide and 5-hydroxymethylfurfural (HMF) in reconstituted potato chips was highly correlated with frying temperature and time. The formation of HMF had significant correlation acrylamide formation. Water activity could also influence the formation of acrylamide and HMF.

Most potato chips and whole potato-based fried snacks sold in Japanese markets showed acrylamide concentration higher than $1000\text{ }\mu\text{g/kg}$ (Yoshida et al. 2005). The concentrations in non-whole potato-based Japanese snacks, including rice crackers and candied sweet potatoes, were less than $350\text{ }\mu\text{g/kg}$. Those in instant precooked noodles were less than $100\text{ }\mu\text{g/kg}$ with only one exception. Acrylamide concentrations in fresh sliced potato crisps in Europe from 2002 to 2011

based on a dataset of 40,455 samples showed a clear, significant downward trend for mean levels of acrylamide, from 763 ± 91.1 ng/g (parts per billion) in 2002 to 358 ± 2.5 ng/g in 2011; this was a decrease of $53 \% \pm 13.5 \%$ (Powers et al. 2013). The effect of seasonality arising from the influence of potato storage on acrylamide levels was evident, with acrylamide in the first 6 months of the year being significantly higher than in the second 6 months. The proportion of samples containing acrylamide at a level above the indicative value of 1000 ng/g for potato crisps introduced by the European Commission in 2011 fell from 23.8 % in 2002 to 3.2 % in 2011. The limit of detection and limit of quantification of acrylamide found in 32 samples of potato chips purchased on the South Italian market in 2009 were 6 µg/kg and 18 µg/kg, respectively, and recovery values ranged from 90.7 to 96.3 % (Tateo et al. 2010). The relative standard deviation (RSD) ranged between 2.1 % and 5.8 %. The values ranged between 27 and 1400 µg/kg and the arithmetic mean acrylamide content resulted 363 µg/kg. Considering 500 µg/kg as the minimum level possible with the actual available mitigation tools, the number of samples showing an acrylamide level higher than 500 µg/kg resulted to be 22 %.

Maillard reaction had been found to produce melanoidin pigments and a host of aroma and flavour volatiles including heterocyclic compounds such as pyrazines, pyrroles, furans, oxazoles, thiazoles and thiophenes (Mottram et al. 2002; Halford et al. 2012), but if free asparagine participated in the final stages, it resulted in the production of acrylamide, an undesirable contaminant (Muttucumaru et al. 2014b).

Mycotoxins in Diseased Potatoes

Potato tubers artificially infected with *Fusarium sambucinum* were contaminated with the mycotoxin, diacetoxyscirpenol, in concentrations up to 200 µg/tuber (Ellner 2002). The toxin could also be found in tubers without any disease symptoms. *Fusarium graminearum*, causal pathogen of potato dry rot, produced trichothecene mycotoxins in diseased tissues (Delgado et al. 2010). Xue et al. (2013) detected two type A (T-2 and

diacetoxyscirpenol) and two type B (3-acetyldeoxynivalenol and Fusarenon X) trichothecenes in potato tubers inoculated with *Fusarium sulphureum*. It was found that T-2, diacetoxyscirpenol, 3-acetyldeoxynivalenol and Fusarenon X could be predominantly detected in diseased lesion, and the toxin could also be identified in tubers without any disease symptoms. Four trichothecenes (Fus-X, 3ADON, DAS and T-2) were detected in potato tubers inoculated with *Fusarium* spp. (Xue et al. 2014). The trichothecenes were found not only in the lesion but also in the adjacent asymptomatic tissue.

Potato Consumption, Nutrition and Health

In a secondary analysis of 24-h dietary recall data from the National Health and Nutrition Examination Survey (NHANES) 2003–2006, Freedman and Keast (2011) found that approximately 35 % of American children and adolescents consumed white potatoes (WP), oven-baked fries (OBF) and French fries (FF) and 18 % consumed FF. Intakes were lower in children compared with adolescents. Among adolescents, more boys than girls consumed FF. Both WP+FF+OBF and FF provided 9–12 % of total daily energy (but was within energy requirements in the highest consumers); 8–15 % of daily fat (>75 % monounsaturated fatty acids+polyunsaturated fatty acids); ≥ 10 % dietary fibre, vitamin B6 and potassium; 5 % or greater thiamine, niacin, vitamin K, phosphorus, magnesium and copper; and less than 5 % sodium intake, for all sex–age groups. The combination WP+FF+OBF provided 5 % or greater vitamin C for all sex–age groups and 5 % or greater vitamin E and iron for most groups; FF provided 5 % or greater vitamin E intakes for all. They found that approximately 35 % of adults consumed potatoes; 12 % consumed FF (Freedman and Keast 2012). Intakes were lowest in adults aged 51+ years. More males, compared to females, consumed potatoes. In all age–sex groups, potatoes and FF provided 7–11 % of total energy (within daily energy requirements); 3–14 % of daily fat (>75 %

MUFA+PUFA); >15 % dietary fibre, >13 % vitamin B6 and potassium; >5 % thiamine, niacin, phosphorus, magnesium and copper; and <5 % sodium. Potatoes provided >10 % vitamin C for all age–sex groups and >5 % vitamin K and iron for most groups; FF provided >5 % vitamin E and folate intakes for all. These cross-sectional data show that WP, including FF, provided short-fall nutrients within energy requirements to children and adolescents and, when consumed in moderate amounts, can be part of healthful diets.

Gibson and Kurilich (2013) found that, in a secondary analysis of 4-day dietary records from the British National Diet and Nutrition Survey 2008–2011, over 92 % of respondents consumed potatoes [oven chips, fried chips, boiled potatoes, mashed potatoes, roast potatoes and jacket (baked) potatoes], 27 % consumed oven chips and 41 % consumed fried chips. Potatoes (including chips) contributed 7 % of total energy, but greater proportions of potassium and vitamin B6 (15 %), vitamin C (14 %), fibre (13 %), folate (10 %) and magnesium (9 %). In contrast, they contributed only 4 % of saturated fatty acids. Among UK adults, potatoes provided in total 7 %, 10 % and 13 % of monounsaturated fatty acid, n-6polyunsaturated fatty acid and n-3 polyunsaturated fatty acid in the diet, respectively, compared with only 4 % of saturated fatty acid and 6 % of total fatty acids. Fried chips were more popular than oven chips, being consumed by 41 % of the total sample and half of all teenagers. It was concluded that potatoes, as currently consumed in their various forms, enriched the diet in this population in respect of at least five micronutrients, including potassium, magnesium, folate, vitamin C and vitamin B6, as well as dietary fibre and unsaturated fatty acids, while lowering the dietary concentration of saturated fat. Potatoes can increase the nutrient density of the diet by providing a relatively high micronutrient contribution, compared with energy content, while delivering only modest amounts of saturated fatty acid and sodium. Nutritionally, potatoes and potato products should be seen as a white vegetable, whose consumption should be encouraged alongside other, coloured, vegetable.

Potatoes (*Solanum tuberosum*) are an important food crop worldwide and contribute key nutrients to the diet, including vitamin C, potassium and dietary fibre (McGill et al. 2013). Potatoes and potato components have been shown to have favourable impacts on several measures of cardiometabolic health in animals and humans, including lowering blood pressure, improving lipid profiles and decreasing markers of inflammation.

Antioxidant Activity

Under active oxidation conditions, 20 g soy oil treated with 0.05 g of freeze-dried potato peel extracts attained lower peroxide values (22.0–28.0 meq/kg) than the control oil sample (109.0 meq/kg) indicating very strong antioxidant activities (Onyeneho and Hettiarachchy 1993). The antioxidant activities of these extracts were due to the presence of phenolic acids, namely, chlorogenic, protocatechuic and caffeic acids that were predominant and appeared to be mainly responsible for the strong antioxidant activities of the extracts. Potato peel extracts, at various concentrations, exhibited very strong antioxidant activity in refined soybean oil, which was almost equal to synthetic antioxidants BHT (butyl-hydroxytoluene) and BHA (butyl-hydroxyanisole) (Zia-ur-Rehman et al. 2004). The results suggested that potato peel extract in oils, fats and other food products could safely be used as natural antioxidant to suppress lipid oxidation. After 4 day storage at 63 °C, 5.00 g of sunflower oil containing either the freeze-dried potato peel waste extract (200 ppm) or BHA (200 ppm) reached peroxide values (PV) of 37.38 and 37.47 meq/kg, respectively (De Sotillo et al. 1994b). The freeze-dried potato peel waste extract was as good as BHA as antioxidant. The freeze-dried potato peel waste extract was as good as BHA as antioxidant. After 16 day storage at 63 °C, 5.00 g of soybean oil containing either the methanolic potato peel extract (800, 1600 ppm) or BHA (200 ppm) and BHT (200 ppm) reached peroxide values (PV) of 37.35, 24.65, 33.20 and 28.88 meq/kg, respec-

tively (Samarin et al. 2012). Also the Rancimat method revealed that TBHQ (t-butylhydroxyquinone) was the best antioxidant, but potato peel extract was as good as BHA and BHT. Potato peel extracted with menthol had the highest amount of phenolic compounds.

The free- and bound-form phenolics in potato peel showed high DPPH radical scavenging activity, while those in the flesh showed low activity (Nara et al. 2006). The total amount of chlorogenic acid and caffeic acid in the free-form phenolics from the peel was highly correlated with the DPPH radical scavenging activity. Ferulic acid was identified as the active radical scavenging compound in the bound-form phenolics from the peel. Studies found that potato peel (PE) was capable of protecting erythrocytes against oxidative damage probably by acting as a strong antioxidant (Singh and Rajini 2008). PE was found to inhibit lipid peroxidation with similar effectiveness in both rat RBCs and human RBC membranes (about 80–85 % inhibition by PPE at 2.5 mg/ml). While PE per se did not cause any morphological alteration in the erythrocytes, under the experimental conditions, PE significantly inhibited the H_2O_2 -induced morphological alterations in rat RBCs and was found to offer significant protection to human erythrocyte membrane proteins from oxidative damage induced by ferrous ascorbate. Methanolic extract of potato peels showed potent antioxidant activity in antioxidant assays and under accelerated oxidation conditions using sunflower oil as oxidation substrates for 72 h at 70 °C (Mohdaly et al. 2010, 2013). The potent antioxidant activity of potato peels could be attributed to its high content of phenolic compounds and flavonoids. The results suggested that potato peels could be used as preservative ingredients in the food and/or pharmaceutical industries. The main phenolic compounds identified in potato peel waste extracts were chlorogenic and ferulic acids; small amounts of gallic and hydroxycinnamic acids were also found (Amado et al. 2014). Potato peel extracts were able to stabilise soybean oil under accelerated oxidation conditions, minimising peroxide, totox and p-anisidine indices. Their results demonstrated potato peel waste to be a good source of

antioxidants for effectively limiting oil oxidation while contributing to the revalorisation of these agrifood by-products.

Patatin purified from potato tuber showed antioxidant or antiradical activity by a series of in-vitro tests, including 1,1-diphenyl-2-picrylhydrazyl (DPPH) radical ($IC_{50}=0.582$ mg/mL) scavenging activity assays, anti-human low-density lipoprotein peroxidation tests and protections against hydroxyl radical-mediated DNA damages and peroxynitrite-mediated dihydrorhodamine 123 oxidations (Liu et al. 2003). It was suggested that cysteine and tryptophan residues in patatin might contribute to its antioxidant activities against radicals. Patatin from potato fruit was found to possess significant antioxidant activities measured by scavenging of the DPPH and superoxide free radicals, notable reducing power, protective effects against hydroxyl radical-induced oxidative DNA damage and lipid peroxidation inhibition (Sun et al. 2013).

Antioxidant activity varied among potato cultivars but was not related to flesh colour or total phenolics (Al-Saikhan et al. 1995). The antioxidant activity for white-flesh cultivars ranged from 65.2 to 88.1 % inhibition relative to control and total phenolics of 369.1–527.1 μ g/g. The antioxidant activity for yellow-flesh cultivars ranged from 68.6 to 89.2 % inhibition relative to control and total phenolics of 237.7–407 μ g/g. Antioxidant activity was evenly distributed within tuber parts and/or sections, except for skin tissue which had the greatest antioxidant activity and total phenolic content. Total phenolics varied among cultivars, with some containing twofold higher concentrations than other cultivars. Phenolic content differences were genotype dependent and not related to flesh colour.

Total anthocyanin ranged from 6.9 to 35 mg per 100 g fresh weight in the red-fleshed and 5.5 to 17.1 in the purple-fleshed clones (Brown et al. 2003). Red-fleshed clones contained predominantly acylated glycosides of pelargonidin, while the purple-fleshed clones contained a more complex content of acylated glucosides of pelargonidin, petunidin, cyanidin and malvidin but had predominantly acylated glycosides of petunidin and peonidin. Oxygen radical absorbance capac-

ity and ferrous reducing ability of plasma revealed that the antioxidant levels in the red- or purple-fleshed potatoes were two to three times higher than white-fleshed potato. In potatoes with total carotenoids ranging from 35 to 795 µg per 100 g FW, the lipophilic extract of potato flesh presented oxygen radical absorbance capacity (ORAC) values ranging from 4.6 to 15.3 nmoles α-tocopherol equivalents per 100 g FW (Brown 2005). The hydrophilic antioxidant activity of solidly pigmented red or purple potatoes was comparable to brussels sprouts or spinach. In red and purple potatoes with solidly pigmented flesh with levels of total anthocyanin ranging from 9 to 38 mg per 100 g FW, ORAC ranged from 7.6 and 14.2 umole per g FW of trolox equivalents. Potato contained an average 20 mg per 100 g FW of vitamin C, which may account for up to 13 % of the total antioxidant capacity. Potatoes should be considered vegetables that may have high antioxidant capacity depending on the flesh composition. Potato anthocyanins were reported to be potent antioxidants and anti-inflammatory substances (Brown et al. 2008). The level of total anthocyanins is correlated with antioxidant level ($R^2=0.94$). Several methods of cooking interacted with genotypes in the antioxidant level remaining after cooking compared to raw potatoes. No method of cooking completely eliminated antioxidant activity, while boiling appeared to increase it compared to raw potato in the case of the most highly pigmented clone.

The main potato antioxidants were reported to be polyphenols, ascorbic acid, carotenoids, tocopherols, α-lipoic acid and selenium (Lachman and Hamouz 2005). Polyphenolic antioxidants found in potatoes were L-tyrosine, caffeic acid, scopolin, chlorogenic and cryptochlorogenic acid and ferulic acid. In addition, red and purple potatoes contained acylated anthocyanins and pigmented potatoes displaying two to three times higher antioxidant potential in comparison with white-fleshed potato. Red potato tubers contained glycosides of pelargonidin and peonidin, and purple potatoes contained glycosides of malvidin and petunidin. Anthocyanins containing petunidin showed greater antioxidant potential than those with malvidin, peonidin or

pelargonidin. Total anthocyanins (TAC) in coloured-fleshed potato cultivars ranged from 248.5 to 2257.8 mg/kg dry matter (Lachman et al. 2012). Cold storage (4 °C) influenced TAC differentially. In the Violette and Highland Burgundy Red cultivars, TAC increased by 18.5 % and 12.1 %, respectively, and in the Valfi cultivar, it decreased by 33.9 %. Baking increased TAC 3.34 times, whereas cooking in boiled water increased it 4.22 times. Correlation between antioxidant activity (AOA) and TAC ($R^2=0.659$) was found. Violette, Vitelotte and Highland Burgundy Red cultivars with the highest TAC showed high AOA, and the Shetland Black cultivar and the cultivars Salad Blue and Blue Congo with a marbled texture showed the lowest TAC and AOA.

Total anthocyanin (ACY) and total phenolic (PHEN) contents of different purple- and red-fleshed potato genotypes ranged from 11 to 174 mg cyanidin-3-glucoside/100 g fresh weight and from 76- to 181-mg chlorogenic acid/100 g fresh weight, respectively, and were genotype and location dependent (Reyes et al. 2005). Although ACY and PHEN concentrations in potato peel were 0.9- to 1.6-fold higher than in potato flesh, overall contribution of the peel to ACY and PHEN contents of a potato slice was ~20 %. High positive correlations between antioxidant capacity and ACY and PHEN suggested that these compounds were mainly responsible for the antioxidant capacity. The hydrophilic oxygen radical absorbance capacity (ORAC) and antioxidant capacity of 74 potato genotypes ranged from 28.25 to 250.67 µmol of trolox equiv/g of DW (Andre et al. 2007a). Total phenolic content varied between 1.12 and 12.37 mg of gallic acid equiv/g of DW, total carotenoid content between 2.83 and 36.21 µg/g of DW and total vitamin C content between 217.70 and 689.47 µg/g of DW. The hydrophilic antioxidant capacity and the total phenolic content were highly and positively correlated ($R^2=0.91$). The iron content ranged from 29.87 to 157.96 µg/g of dry weight (DW), the zinc content from 12.6 to 28.83 µg/g of DW and the calcium content from 271.09 to 1092.93 µg/g of DW. A strong relationship between iron and calcium contents was also found ($R^2=0.67$). Total anthocyanin of 38 native

potato cultivars from South America ranged from zero to 23 mg cyanidin equivalents/100 g fresh weight (FW) (Brown et al. 2007). The cultivars consisted of 23 diploids, seven triploids and eight tetraploids. Total carotenoid ranged from 38 to 2020 μg zeaxanthin equivalents/100 g FW. Oxygen radical absorbance capacity (ORAC) was measured for the anthocyanin (hydrophilic) and carotenoid (lipophilic) extracts. The hydrophilic ORAC ranged from 333 to 1408 μM trolox equivalents/100 g FW. The lipophilic ORAC ranged from 4.7 to 30 nM α -tocopherol equivalents/100 g FW. Total carotenoids were negatively correlated with total anthocyanins. Total anthocyanins were correlated with hydrophilic ORAC. Among clones with less than 2 mg cyanidin equivalents/100 g FW, total carotenoid and lipophilic ORAC were correlated, but this was not true for analysis of all 38 clones.

Total antioxidant activity (AA) of Texas specialty (coloured) potato selections ranged from 157 μg trolox equivalents (TE)/gfw to 832 μg TE/gfw and 810 μg TE/gfw to 1622 μg TE/gfw using the DPPH and ABTS assays, respectively (Reddivari et al. 2007a). TP total phenolic content (TP) ranged from 221 μg chlorogenic acid equivalents (CGAE)/gfw to 1252 μg CGAE/gfw. Selection COH2F2-2P/P had the highest AA and TP. Purple flesh selections had the highest AA and TP, followed by red-flesh and yellow-flesh selections. Selections with similar flesh colour did not differ significantly in AA and TP. A significant positive correlation was observed between AA and TP. Chlorogenic acid, gallic acid, catechin, caffeic acid and malvidin-3-(*p*-coumaroyl rutinoside)-5-galactoside were the major polyphenols identified. Chlorogenic acid accounted for 50 to 70 % of TP, followed by catechin, gallic acid and caffeic acid. Chlorogenic acid contributed 28 to 45 % to AA, followed by gallic acid, catechin and caffeic acid. Reddivari et al. (2007b) found that the antioxidant activity (AOA), total phenolics (TP) and total carotenoids (TC) of 25 potato genotypes differed significantly with genotype (G), Texas location (L) and year (Y). Phenolic composition differed significantly among genotypes and between locations. The AOA, TP and chlorogenic acid content were

significantly correlated with one another. Genotypic effects were significant for all parameters measured and were larger than location and year effects. Interaction effects (G \times L and G \times L \times Y) were significant for most parameters, but were relatively smaller than genotypic effects. Lutein and violaxanthin were the major carotenoids identified, and genotypes differed significantly in their carotenoid content.

Potatoes pan-fried in sunflower oil, olive oil and refined palm oil enriched with olive leaf polyphenols were found to have higher DPPH radical scavenging capacity and higher total polyphenols, tocopherols, phytosterols and squalene content than those pan-fried in the non-supplemented oils (Chiou et al. 2009). Oleuropein as well as other polyphenol compounds were detected in all French fries cooked in enriched oils (Chiou et al. 2007). Polyphenol intake by consuming French fries pan-fried in the enriched oils was calculated to be 6 to 31 times higher than that in the case of French fries fried in non-enriched commercial oils, being dependent on the frying oil type.

Antioxidant capacity of potato was influenced by potato variety and cooking conditions; however, cooked potatoes retained 68–97 % oxygen radical absorbance capacity assay (ORAC) value depending on cooking procedure and variety (Xu et al. 2009). Chlorogenic acid and its isomers dominated the phenolic composition of each variety involved in this study. ORAC and total phenolics were highly and positively correlated ($R^2=0.9119$). Principal component analysis that showed different cooking processes did not influence the trend of the antioxidant profile of the eight potato varieties, but specific compounds exerted influence on the antioxidant capacity. The effects of drought stress on dietary antioxidant and glycoalkaloid contents in potato tubers of five native Andean cultivars were highly cultivar specific (Andre et al. 2009). The antioxidant contents of the yellow tuber-bearing cultivars (Sipancachi and SS-2613) were weakly affected by the drought treatment, whereas the pigmented cultivars demonstrated highly cultivar-dependent variations. A drastic reduction of anthocyanins and other polyphenols was observed in the red-

(Sullu) and purple-fleshed (Guincho Negra) cultivars, whereas an increase was shown in the purple-skinned and yellow-fleshed cultivar (Huata Colorada). The hydrophilic antioxidant capacity (evaluated by Folin-Ciocalteu and H-oxygen radical absorbance capacity assays) was highly correlated with the polyphenol content and followed, therefore, the same behaviour upon drought. Carotenoid contents, including β -carotene, as well as vitamin E, tended to increase or remain stable following drought exposure, except for the cultivar Sullu, in which the level of these lipophilic antioxidants was decreased. Vitamin C contents were not affected by drought with the exception of Guincho Negra, in which the level was increased. These variations of health-promoting compounds were associated with increased or stable levels of the toxic glycoalkaloids, α -solanine and α -chaconine. Storage at 10 °C for 4 months tended to decrease the concentrations of all dietary antioxidants, except those of vitamin E. This storage also reduced the drought-induced variations observed in freshly harvested tubers.

The total equivalent antioxidant capacity (TEAC) was higher in the extracts of early potato cultivars in Racale, and a highly positive linear relationship ($R^2=0.8193$) between TEAC values and total phenolic content was observed (Leo et al. 2008). There was a considerable variation in carotenoid content and weak differences in the ascorbic acid concentration of the examined cultivars of 'early potato' and between the harvested locations (Racale and Monteroni). Chlorogenic acid and catechin were the major phenols present in potato tuber extracts; a moderate amount of caffeic acid and ferulic acid was also detected. A highly significant linear correlation ($R^2=0.9613$) between total antioxidant capacity (as a sum of peroxyl radicals + peroxynitrite) and total phenol content of methanol/water extracts was established. Chlorogenic acid was the most abundant phenolic and ranged from 22 to 473 mg/100 g dry weight in 50 potato genotypes (Navarre et al. 2011). Rutin and kaempferol-3-rutinoside were the most abundant flavonols. Total phenolics ranged from 1.8 to 11 mg/g DW and antioxidant capacity ranged from 27 to 219 μ mol TE/g DW. Total phe-

nolics and antioxidants in these high-phytonutrient potatoes compared favourably to 15 other analysed vegetables. Total phenolic content of native Chilean potatoes varied in the peeled potato samples from 191 to 1864 mg/100 g DM and from 345 to 2852 mg/100 g DM in unpeeled samples (Kong et al. 2012). Antioxidant activity was higher in unpeeled potatoes and was the highest in the unpeeled NG-6 or 'Bruja' native potato.

Purple-fleshed potato cultivars showed higher total phenol (TP content) (by 60 %) than yellow-fleshed cultivars; antioxidant activity (AA) in purple-fleshed cultivars was twice as high as in yellow-fleshed potatoes (Lachman et al. 2008). A medium linear correlation between TP and AA was found ($R^2=0.747$). Average TP content in yellow-fleshed cultivars was 2.96 GAE (g of gallic acid per kg dm); in purple-fleshed cultivars, it was 4.68 GAE. Average AA in yellow-fleshed cultivars was 11.26 AAE (mg of ascorbic acid equivalent per 100 g dm) and in purple-fleshed cv. 24.79 AAE. Purple potatoes exhibited the highest antioxidant activity; peels were more potent than the flesh and contained higher phenolic content (Albishi et al. 2013). Bound and esterified phenolics contributed as much or even more than the free phenolics to the antioxidant activity of the peels. HPLC data showed the presence of chlorogenic, caffeic, *p*-coumaric and ferulic acids.

All cooking treatments (boiling, baking and microwaving) of white-, yellow-, red- and purple-fleshed potatoes reduced ascorbic and chlorogenic acid contents, total glycoalkaloids, α -chaconine and α -solanine with the exception of total anthocyanins (Lachman et al. 2014). The losses of ascorbic and chlorogenic acids were minimised with boiling and total anthocyanin levels retained the highest. Boiling of peeled tubers decreased contents of total glycoalkaloids (α -chaconine and α -solanine) and appeared as the most favourable among the three tested methods. Moreover, due to higher initial levels, red- and purple-fleshed cultivars retained higher amounts of antioxidants (ascorbic acid, chlorogenic acid and total anthocyanin) after boiling and may be healthier as compared with white or yellow cultivars.

Both red and purple-fleshed potato varieties contained high levels of total polyphenols (227–845 mg/100 g dry weight) and anthocyanins (21–109 mg/100 dry weight) (Kita et al. 2013). The process of frying caused degradation of anthocyanin compounds (38–70 %); pelargonidin and malvidin derivatives were more stable during frying than petunidin derivatives. Although frying process affected the anthocyanin and polyphenol levels, the obtained potato crisps exhibited bright intensive colour and good antioxidant activity as evaluated by 2,2'-azino-bis-3-ethylbenzothiazoline-6-sulphonic acid (ABTS) and 1,1-diphenyl-2-picrylhydrazyl (DPPH) radical as well as ferric reducing ability of plasma (FRAP) assays. In a recent study, they reported both red- and purple-fleshed potato varieties contained higher content of total polyphenols (250–526 mg/100 g DW) and anthocyanins (16–57 mg 100/g DW) (Kita et al. 2014). The higher content of polyphenols was directly related to higher antioxidant activity of tested potatoes. The process of frying caused almost total degradation of anthocyanin compounds, while polyphenols exhibited quite good stability (especially in chips obtained from red-fleshed potatoes). The antioxidant activity decreased significantly in chips obtained from purple-fleshed potatoes. Red-fleshed varieties exhibited better stability after long-term storage and gave chips with better properties.

Anticancer Activity

Among the *Solanum* steroidal glycoalkaloids tested, only solasodine (from solasonine) and α -chaconine exhibited strong cytotoxicity against tested cancer cells in-vitro (Nakamura et al. 1996). Growth inhibition GI_{50} values (μ g/ml) of solasodine (from solasonine) and α -chaconine against the tested cancer cells were, respectively, as follows: PC-6 (lung cancer) 4.6; 1.83 μ g/ml, MCF-7 (breast cancer) 1.62, 1.54 μ g/ml, SW620 (colon cancer) 3.50, 1.46 μ g/ml, NUGC-3 (stomach cancer) 1.47, 1.43 μ g/ml, P388 (mouse leukaemia) 2.18, 1.58 μ g/ml; α -Chacocine was more superior than solasodine and α -solanine against all cancer cell lines. Solanidine α -L-rhamnopyranosyl-

(1 \rightarrow 2)- β -D-glucopyranoside was weaker than α -chacocine and solasodine.

Glycoalkaloids and metabolites of potato inhibited the growth of human colon (HT29) and liver (HepG2) cancer cells (Lee et al. 2004). Four concentrations each (0.1, 1, 10 and 100 μ g/mL) of the potato trisaccharide glycoalkaloids α -chaconine and α -solanine; the disaccharides β (1)-chaconine, β (2)-chaconine and β (2)-solanine; the monosaccharide γ -chaconine and their common aglycone solanidine; the tetrasaccharide potato glycoalkaloid dehydrocommersonine and the potato aglycone demissidine were all antiproliferative, with the glycoalkaloids being the most active and the hydrolysis products less so. The effectiveness against the liver cells was greater than against the colon cells. Potency of α -chaconine at a concentration of 1 μ g/mL against the liver carcinoma cells was higher than those observed with the anticancer drugs doxorubicin and camptothecin. Because α -chaconine and α -solanine also inhibited normal human liver HeLa (Chang) cells, safety considerations should guide the use of these compounds as preventative or therapeutic treatments against carcinomas. Pure α -chaconine and α -solanine from Dejima potatoes and TGA (glycoalkaloids) from five fresh potato varieties (Dejima, Jowon, Sumi, Toya and Vora Valley) tested reduced the numbers of the following human cell lines: cervical (HeLa), liver (HepG2), lymphoma (U937), stomach (AGS and KATO III) cancer cells and normal liver (Chang) cells (Friedman et al. 2005). The results showed that (a) the effects of the glycoalkaloids were concentration dependent in the range of 0.1–10 μ g/mL (0.117–11.7 nmol/mL); (b) α -chaconine was more active than α -solanine; (c) some mixtures exhibited synergistic effects, whereas other produced additive ones; (d) the different cancer cells varied in their susceptibilities to destruction; and (e) the destruction of normal liver cells was generally lower than that of cancer liver cells.

CO112F2-2 potato cultivar extracts and their anthocyanin fraction at 5 μ g chlorogenic acid eq/ml were more active and inhibited cell proliferation and increased the cyclin-dependent kinase inhibitor p27 levels in both LNCaP (androgen

dependent) and PC-3 (androgen independent) prostate cancer cells (Reddivari et al. 2007c). Potato extract and its anthocyanin fraction were found to be cytotoxic to both prostate cancer cells via activation of caspase-independent apoptosis. The apoptosis induced by whole potato extracts in prostate cancer cell lines may be in part due to α -chaconine and gallic acid (Reddivari et al. 2010). α -Chaconine (5 μ g/ml) and gallic acid (15 μ g/ml) exhibited potent antiproliferative properties and increased cyclin-dependent kinase inhibitor p27 levels in both cell lines. Both α -chaconine and gallic acid induced poly[adenosine diphosphate (ADP)] ribose polymerase cleavage and caspase-dependent apoptosis in LNCaP cells; however, caspase-independent apoptosis through nuclear translocation of endonuclease G was observed in both LNCaP and PC-3 cells. The proliferation of human mammalian cancer (MCF-7) cells was significantly inhibited in a dose-dependent manner after exposure to 'early potato' cultivar extracts (Leo et al. 2008).

HepG₂ human hepatocarcinoma cell lines treated with solanine showed typical signs of apoptosis (Gao et al. 2006). Solanine opened up the permeability transition channels in HepG₂ mitochondrial membrane by lowering the membrane potential, leading to Ca²⁺ being transported down its concentration gradient, which in turn led to the rise of the concentration of Ca²⁺ in the cell, turning on the mechanism for apoptosis.

The proliferation of colon cancer and liver cancer cells was significantly inhibited by potato antioxidant extracts (Wang et al. 2011). The highest antiproliferative activity was observed in extracts of *Solanum pinnatisectum* and the lowest in potato cv. Northstar. *S. pinnatisectum* had the highest antioxidant activity, total phenolic and chlorogenic acid content. An inverse correlation was found between total phenolics and the EC₅₀ of colon cancer cell ($R^2=0.9303$), as well as liver cancer cell proliferation ($R^2=0.8992$). The relationship between antioxidant activity and EC₅₀ of colon cancer/liver cancer cell proliferation was significant ($R^2=0.8144$; $R^2=0.956$, respectively). A significant difference in inhibition of cancer cells existed between the 3 polyphenols: chlorogenic acid, pelargonidin chloride and malvidin

chloride, suggesting that chlorogenic acid was a critical factor in the antiproliferation of colon cancer and liver cancer cells.

The results of studies by Madiwale et al. (2011) suggested that although the antioxidant activity and phenolic content of potatoes were increased with storage, the antiproliferative and pro-apoptotic activities against early, HCT-116 and advanced stage, HT-29 human colon cancer cell lines were suppressed. Purple-fleshed potatoes were more potent in suppressing proliferation and elevating apoptosis of colon cancer cells compared with white- and yellow-fleshed potatoes. The extracts from both fresh and stored potatoes (10–30 μ g/mL) suppressed cancer cell proliferation and elevated apoptosis compared with the solvent control, but these anticancer effects were more pronounced with the fresh potatoes. Storage duration had a strong positive correlation with antioxidant activity and percentage of viable cancer cells and a negative correlation with apoptosis induction. Ethanolic extracts of baked and chipped samples suppressed proliferation and elevated apoptosis in human colon HCT-116 (p53 wild type; ras mutated) and HT-29 (p53 mutated; ras wild type) human colon cancer cell lines (Madiwale et al. 2012). Antiproliferative and pro-apoptotic properties of baked potatoes were similar to that of fresh potatoes, while chipping caused a significant suppression. Phenolic content and antioxidant activity of purple-fleshed potatoes, after baking, were comparable with those of anthocyanin-rich berries. When compared with unprocessed samples, baking or chipping led to significant losses in the phenolic and anthocyanin content and antioxidant activity of the potatoes. However, with storage, total phenolic and anthocyanin content and antioxidant activity increased in baked samples, while in the chipped samples they remained constant. Hence, purple-fleshed potatoes could be a healthier choice for consumers as they were found to possess greater levels of bioactive compounds and anticancer properties even after processing as compared with their white- and yellow-fleshed counterparts.

Patatin from potato fruit was identified as a potent antiproliferative agent against mouse mel-

anoma B16 cells, causing cell cycle arrest in the G1 phase (Sun et al. 2013). Assays of apoptotic cells also showed that patatin treatment at concentrations of 20 mg/mL resulted in a marked reduction of viable cells.

Heated potato fibre (Potex) containing melanoidin complexes inhibited C6 glioma cell proliferation in a dose-dependent manner (Langer et al. 2011). High molecular weight components present in initial extract were responsible for stronger antiproliferative effect compared with low molecular weight fraction. It was observed that the activity of melanoidins present in heated Potex was linked to dysregulated MAPK and Akt signalling pathways, as well as to cell cycle cessation. In a subsequent study, they reported that both heated potato fibre Potex extract (180 °C for 2 h) and melanoidins isolated from the extract exert growth-inhibiting activity in human LS180 colon cancer cells in-vitro (Langner et al. 2013). Roasted potato fibre extract (AM4) as well as with high (HMW) and low (LMW) molecular weight fractions (containing melanoidins) isolated from the extract, at concentration of 1000 µg/ml, reduced cell growth down to 45 %, 69 % and 54 %, respectively. Besides deregulation of ERK1/2 signalling upon treatment, multiple alternations in cell cycle regulators activity were found (i.e. cyclinD1, cyclin-dependent kinase 4 and 6, p21, p27, p53, pRb) leading to cell cycle cessation in G0 phase.

Epidemiologic health studies had shown a reduction in cancer risk in individuals and populations consuming high amounts of dietary fibre and vegetables (Cummins et al. 1992; Faivre et al. 1993). Recently, a strong inverse association between starch consumption and incidence of large bowel cancer was reported. Starch being the predominant form of carbohydrate found in potatoes, an appreciable amount of which called resistant starch (RS) had been reported to escape digestion in the small intestine, depending on physical inaccessibility, type of granule and food processing. Starch and dietary fibre together were reported as the principal substrates controlling the pattern of fermentation in the colon and, thus, the metabolism of compounds like bile acids, nitrate and enzyme activities (bacterial and anti-

oxidant enzymes), which had been implicated in carcinogenesis (Cummings et al. 1992; Hylla et al. 1998; Raban et al. 1994). This resistant starch had been reported to have similar physiological effects and health benefits of fibre in that it provides bulk, gives protection against colon cancer, increases glucose tolerance and insulin sensitivity, reduces plasma cholesterol and triglyceride concentrations, enhances satiety and may even reduce fat storage.

Antiviral Activity

The infectivity of herpes simplex virus type I in tissue culture was inhibited by prior incubation with aqueous suspensions of glycoalkaloids in order of activity α -chaconine greater than α -tomatine greater than α -solasanine but not by the corresponding aglycones, solanidine, tomatidine and solasodine (Thorne et al. 1985). The glycones, but not the aglycones, showed cytopathic effects on cellular membranes of Vero cells and erythrocytes; therefore, it was suggested that inactivation of virus results from insertion of the glycones into the viral envelope.

Anti-inflammatory Activity

In a randomised study of free-living healthy men (18–40 years old), consumption of pigmented-fleshed potato was found to alter oxidative stress, DNA damage and inflammatory damage (Kaspar et al. 2011). Compared with the white-fleshed potato (WP) group, the yellow-fleshed potato (YP) group had higher concentrations of phenolic acids and carotenoids, whereas the purple-fleshed potato (PP) group had higher concentrations of phenolic acids and anthocyanins. Men who consumed YP and PP tended to have lower plasma interleukin IL-6 compared with those consuming WP. The PP group tended to have a lower plasma C-reactive protein concentration than the WP group. The plasma 8-hydroxydeoxyguanosine concentration was lower in men who consumed either YP or PP compared with WP. Studies showed that potato glycoalkaloids α -chaconine,

α -solanine and solanidine, along with potato peel extracts, possessed anti-inflammatory effects in-vitro (Kenny et al. 2013). α -Chaconine and solanidine significantly reduced interleukin-2 (IL-2) and interleukin-8 (IL-8) productions in Con A-induced Jurkat cells. In LPS-stimulated RAW macrophages, α -solanine, solanidine and two potato peel extracts significantly reduced induced NO production. Oral administration of *Solanum tuberosum* var. Vitelotte (SV) extract to NC/Nga mice resulted in the inhibition of the development of atopic dermatitis (AD)-like skin lesions induced by the topical application of 2,4-dinitrochlorobenzene (shim and Choung 2014). SV extract has attenuated AD-like skin lesion, ear thickening and scratching behaviour and alleviated infiltrated inflammatory cells in tissue. Production of Th1 and Th2 cytokines was inhibited in splenocyte cultures. Additionally, reduced levels of IgE and IgG1/IgG2a ratio in serum and expression of AD-related mRNAs in lesional skins were observed in SV-treated mice compared with control group. The chloroform fraction of the peel of Jayoung (CFPJ), a color-fleshed potato, inhibited the expressions of inducible nitric oxide synthase (iNOS) and cyclooxygenase-2 (COX-2) at the transcription level and attenuated the transcriptional activity of nuclear factor- κ B (NF- κ B) by reducing the translocation of NF- κ B depending on degradation of inhibitory κ B- α (I κ B- α) in lipopolysaccharide (LPS)-induced RAW 264.7 macrophages (Lee et al. 2014). Additionally, CFPJ attenuated the phosphorylations of mitogen-activated protein kinase 3/6 (MKK3/6) and of p38. Administration of CFPJ to mice with dextran sulphate sodium-induced colitis significantly reduced the severity of colitis and the productions and protein levels of pro-inflammatory mediators in colonic tissue.

Antidiabetic Activity

Potato peel (PP) powder supplementation in diet was found to effectively attenuate diabetic alterations in rats (Singh et al. 2005a). Streptozotocin diabetic rats fed with PP powder-supplemented diet for 4 weeks showed a significant decrease in

blood glucose levels. Incorporation of PP powder reduced significantly the hypertrophy of both the liver and kidney of streptozotocin (STZ)-diabetic rats and also normalised the activities of serum ALT and AST, hepatic and renal MDA and GSH, as well as activities of various antioxidant enzymes in the liver and kidney of diabetic rats. Furthermore, PP powder in the diet also appeared to attenuate the eye lens damage associated with the diabetic condition. They also reported that in a 4-week feeding trial, incorporation of potato peel powder (5 and 10 %) in the diet of diabetic rats was found to significantly reduce the plasma glucose level and also reduce drastically the polyuria of STZ diabetic rats (Singh et al. 2005b). The total food intake was significantly reduced in the diabetic rats fed 10 % PP powder compared to the control diabetic rats. However, the body weight gain over 28 days was nearly four times greater in PP powder-supplemented diabetic rats (both at 5 and 10 %) compared to the control diabetic rats. PP powder in the diet also decreased the elevated activities of serum transaminases (ALT and AST) and nearly normalised the hepatic MDA and GSH levels as well as the activities of specific antioxidant enzymes in the liver of diabetic rats.

Calystegines A₃ and B₂ purified from potatoes were found to inhibit maltase and sucrose, α -glucosidases contributing to human carbohydrate degradation in the small intestine (Jocković, et al. 2013). Calystegine A₃ showed low in-vitro enzyme inhibition; calystegine B₂ inhibited mainly sucrose activity. Both compounds were not transported by Caco-2 cells indicating low systemic availability. The authors suggested that vegetables rich in calystegine B₂ should be further investigated as possible components of a diet preventing a steep increase in blood glucose after a carbohydrate-rich meal.

Feeding mice with polyphenolic-rich potato extracts (PRPE) of cultivars Onaway and Russet Burbank for 10 weeks attenuated weight gain in male and female mice by as much as 63.2 %, which was associated mostly with a reduction in adiposity (Kubow et al. 2014). Mice receiving PRPE showed enhanced capacity for blood glucose clearance. Sex differences regarding the

impact of HFD and PRPE on plasma levels of insulin, ghrelin, leptin, gastric inhibitory peptide and resistin were observed. PRPE may serve as part of a preventative dietary strategy against the development of obesity and type 2 diabetes.

Starch in foods may be classified into rapidly digestible starch (RDS), slowly digestible starch (SDS) and resistant starch (RS) (Englyst et al. 1992). RS may be further divided into three categories according to the reason for resistance to digestion. Studies conducted showed that the replacement of digestible starch with RS resulted in significant reductions in postprandial glycaemia and insulinemia and in the subjective sensations of satiety (Raban et al. 1994). The amount of resistant starch found in potatoes was highly dependent upon preparation methods. Cooking and then cooling potatoes significantly increased resistant starch. For example, cooked potato starch contained about 7 % resistant starch, which increased to about 13 % upon cooling (Englyst et al. 1992). Cooked potatoes were found to have high levels of digestible starch (DS) (García-Alonso and Goñi 2000). Starch digestibility is improved after processing and it is affected by the cooking methods. Boiled and mashed potatoes showed the highest rate of digestion; on the contrary raw potato was hardly digested. The estimated glycaemic index (GI) from the degree of starch hydrolysis within 90 min was in accordance with the reported GI values, for potatoes processed in the same way. Results of studies demonstrated that degree of gelatinisation (DG) of starch strongly affected its digestibility in-vitro and may influence the postprandial glycaemic response (Parada and Aguilera 2009). DG was closely related with heating temperature ($R^2=0.997$), size parameters of granules (measured by image analysis), in-vitro digestion and in-vivo glycaemic response (R^2 of adjusted models >0.9). Shape parameters of granules were not related with the degree of gelatinisation. Seven potato cultivars tested had a wide range of GI values (53–103) (Ek et al. 2014). The Carisma cultivar was classified as low GI and the Nicola cultivar (GI=69) as medium GI, and the other five cultivars were classified as high GI according to ISO guidelines. The GI values were strongly

and positively correlated with the percentage of in-vitro enzymatic hydrolysis of starch in the cooked potatoes. Amylose, dietary fibre and total starch content were not correlated with either in-vitro starch digestibility or GI.

Recently, it was reported that hydrolysis of the potato protein isolates (breaking down of the compound by reacting with water) produced proteins with an increased activity for ACE (angiotensin-I-converting enzyme) inhibition and radical scavenging activity. ACE inhibitors act by inhibiting the conversion of angiotensin I to the potent vasoconstrictor, angiotensin II, thereby improving blood flow and blood pressure. The study suggested that potato was a promising source for the production of bioactive compounds as ingredients for developing functional foods with a beneficial impact on cardiovascular health. ACE inhibitors made by drug companies have been found to be beneficial in treating hypertension, particularly in patients with type 1 or type 2 diabetes, and also appear to provide good cardiovascular and renal protection.

On the negative side, potato is regarded as high glycaemic index (GI) food and is avoided by people following a 'low GI' eating regimen. The GI of potatoes can vary considerably depending on the potato variety (i.e. red vs. russet vs. white vs. Prince Edward), preparation methods (i.e. cooking method, whether it is eaten hot or cold, whether it is mashed or cubed or consumed whole, etc.) and with what is consumed (i.e. the addition of various high fat or high protein toppings). US Russet potatoes have only a moderately high glycaemic index. Individuals who wish to minimise dietary glycaemic index can be advised to precook potatoes and consume them cold or reheated (Fernandes et al. 2005). Boiled potatoes were more satiating than French fries on an energy-equivalent basis, the effect being most prominent in the early postprandial phase, whereas no difference in satiety could be seen on a carbohydrate-equivalent basis. French fries resulted in a significantly lower glycaemic response (glycaemic index (GI)=77) than boiled potatoes either with or without the addition of oil (Leeman et al. 2008). It was also shown that the high glycaemic and insulinaemic features com-

monly associated with potato meals can be reduced by the use of vinegar dressing and/or by serving cold potato products.

Clinical Studies

In a study of ten healthy, normal-weight, young males, after administration of a meal of 50 g raw potato starch (54 % resistant starch (RS)) together with 500 g artificially sweetened syrup, postprandial plasma concentrations of glucose, lactate, insulin, gastric inhibitory polypeptide (GIP), glucagon-like peptide-1 and epinephrine were significantly lower compared with after the meal of 50 g pregelatinised starch (0 % RS) together with 500-g artificially sweetened syrup (Raben et al. 1994). It was concluded that replacement of digestible starch with resistant starch resulted in significant reductions in postprandial glycaemia and insulinemia and in the subjective sensations of satiety. In a subsequent study of 11 healthy, normal-weight, young men, they compared two chemically modified starches—a 1–2 % acetylated potato starch and a starch enriched with 2 % β -cyclodextrin—and a native, unmodified potato starch (control) (Raben et al. 1997). The meal was given in the morning after a 2-day carbohydrate-rich, weight-maintenance diet. After the modified-starch meals, response patterns for plasma glucose, insulin, gastric inhibitory polypeptide, subjective satiety and fullness were significantly different from response patterns after the meal with the control starch. A flattening of the glucose curve, a lower insulin and gastric inhibitory polypeptide response and higher fullness ratings were observed after the meal with the β -cyclodextrin starch. Satiety ratings were higher after both meals with modified starch than after the meal with the control starch. It was concluded that a minor modification insulinaemic (1–2 %) of native potato starch improved the glycaemia, insulinaemic and satiating properties of a meal. In a study of 10 healthy volunteers, potatoes, regardless of variety, cooking method and maturity, were found to have exceptionally high glycaemic index (GI) values (Soh and Brand-Miller 1999). Mean GI values ranged from 65 for canned new potatoes to 10 for boiled Desiree potatoes. The relative lower values of

new potatoes were attributed to differences in starch structure. Cold storage and addition of vinegar reduced acute glycaemia and insulinaemia in healthy subjects after a potato meal (Leeman et al. 2005). Cold storage of boiled potatoes increased resistant starch (RS) content significantly. The results showed that the high glycaemic and insulinaemic features commonly associated with potato meals could be reduced by use of vinegar dressing and/or by serving cold potato products. Precooked Russet potatoes elicited lower area under the curve than day cooked in human subjects, while precooking had no effect on boiled white potatoes (Fernandes et al. 2005). The glycaemic index values of potatoes varied significantly, depending on the variety and cooking method used ranging from intermediate (boiled red potatoes consumed cold: 56) to moderately high (roasted California white potatoes: 72; baked US Russet potatoes: 77) to high (instant mashed potatoes: 88; boiled red potatoes: 89). In studies of healthy subjects, boiled potatoes induced higher subjective satiety than French fries when compared on an energy-equivalent basis (Leeman et al. 2008). French fries elicited the lowest early glycaemic response and was less satiating in the early postprandial phase (area under the curve (AUC) 0–45 min). No differences were found in glycaemic or satiety response between boiled or mashed potatoes. In a second study, French fries resulted in a significantly lower glycaemic response (glycaemic index (GI) =77) than boiled potatoes either with or without the addition of oil (GI=131 and 111, respectively). No differences were found in subjective satiety response between the products served on carbohydrate equivalence.

In a randomised block design study of 9 healthy volunteers, administration of pigmented potatoes resulted in no significant differences in areas under the curve (AUC) for blood glucose response or insulin among the various potatoes studied (Ramdath et al. 2014) Although the mean GI values for the potato types varied (purple=77.0; red=78.0; yellow=81.0; and white=93.0), these differences were not significantly different. The mean polyphenol content (mg GAE/100 g DW) was 234, 190, 108 and 82

for purple, red, yellow and white potatoes, respectively. There was a significant inverse correlation between polyphenol content and GI of the potatoes ($R^2 = -0.825$). In-vitro, polyphenol extracts of red and purple potatoes inhibited α -glucosidase by 37.4 % and 28.7 %, respectively. The GI of coloured potatoes was significantly related to their polyphenol content, possibly mediated through an inhibitory effect of anthocyanins on intestinal α -glucosidase.

Hepatoprotective Activity

Administration of red potato extract (RPE) protected liver damage in D-galactosamine (GalN)-intoxicated rats (Han et al. 2006a). Increases in serum aspartate aminotransferase, alanine aminotransferase and lactate dehydrogenase activities, all of which were induced by GalN injection, decreased in RPE-administered rats, suggesting that RPE acted as a functional food showing anti-hepatotoxicity. Purple potato flakes were found to have antioxidant functions with regard to DDPH radical scavenging activity and inhibition of linoleic acid oxidation, and they improved the antioxidant potentials in rats by enhancing hepatic Mn-SOD (superoxide dismutase), Cu/Zn-SOD and glutathione peroxidase (GSH-Px) mRNA expression (Han et al. 2006b). In another study, Han et al. (2007b) found serum thiobarbituric acid-reactive substances concentration and hepatic superoxide dismutase mRNA level in rats fed red potato flakes (RPF) were significantly lower and higher, respectively, than those in control rats. The results suggested that RPF might improve the antioxidant system by enhancing hepatic SOD mRNA.

Supplementation with anthocyanin-rich purple potato (cv. Shadow Queen) flakes in F344 rats fed a cholesterol-rich diet was found to enhance the antioxidant status (Han et al. 2007a). Thiobarbituric acid-reactive substance (TBARS) levels in the serum and liver of rats fed Shadow Queen were significantly lower than those in the control and white potato (cv. Toyoshiro) groups. The hepatic glutathione levels and activities of hepatic glutathione reductase and glutathione S-transferase in the Shadow Queen were signifi-

cantly higher in the Shadow Queen group than in the control group. The results showed that enhancement of antioxidant enzymes and oxidative status in the serum and liver by the purple potato flake diet (Shadow Queen) containing polyphenols/anthocyanins may play an important role in the protection against adverse effects related to oxidative damage in rats fed a high-cholesterol diet.

Antihypercholesterolemic Activity

Feeding rats a potato-enriched diet for 3 weeks led to a significant decrease in cholesterol and triglyceride levels in plasma and cholesterol level in the liver (Robert et al. 2006). Antioxidant status was also improved by potato consumption. TBARS levels in the heart were decreased and vitamin E/triglycerides ratio in plasma was improved. Robert et al. (2008) found that the consumption of complex carbohydrates (provided as cooked potatoes) by rats for 3 weeks, in combination with different antioxidant micronutrients, may enhance the antioxidant defences and improve lipid metabolism, when compared with starch (complex carbohydrates) and to sucrose consumption (source of simple sugar). Feeding rats a potato-based diet for 3 weeks led to a decrease in cholesterol (−37 %, potato vs. control, and −32 %, potato vs. sucrose) and triglycerides (−31 %, potato vs. control, and −43 %, potato vs. sucrose) concentrations in triglyceride-rich lipoprotein (TGRLP) fractions. The antioxidant status was decreased by sucrose consumption and improved by potato consumption. These effects limited oxidative stress and reduced the risk of developing the associated degenerative diseases, including cardiovascular disease, and could have potential in cardiovascular disease prevention.

Hypotensive Activity

In a crossover study, 18 hypertensive subjects with an average body mass index (BMI) of 29 and administration of six to eight small microwaved purple potatoes twice daily for 4 weeks elicited a significant decrease in diastolic and systolic blood

pressures (Vinson et al. 2012). There was no significant effect of potato on fasting plasma glucose, lipids or HbA1c. There was no significant body weight increase. In a comparative single-dose study six to eight microwaved potatoes with skins and comparable amount of refined potato starch as cooked biscuits given to eight normal fasting subjects, potato caused an increase in plasma and urine antioxidant capacity, whereas refined potato starch caused a decrease in both, i.e. it acted as a pro-oxidant.

Wound Healing Activity

Compared with treatment with plain gauze dressings for burn wounds, the application of the potato peel dressing reduced or eliminated desiccation, permitted the survival of superficial skin cells and hastened epithelial regeneration (Keswani et al. 1990). Bacteriological studies showed that the potato peels had no intrinsic antibacterial activity, the wounds beneath both dressings showing either no growth or, on most occasions, the same bacterial species. The easy availability of potato peels and gauze bandages on to which they can be affixed, the simplicity of the preparation of this dressing, the ease of sterilisation and its low cost of production make this the dressing of choice for burn wounds in developing country. In a series of experiments, full thickness skin defects in 68 rats were covered with dressings made of boiled potato peels, the wounds closed within 14 days, and histologically complete repair of epidermis was found (Dattatreya et al. 1991). The cork layer of the potato peel prevented dehydration of the wound and protected against exogenous agents. Experiments with homogenates revealed that a complete structure of the peel was necessary. Steroidal glycosides may have contributed to the favourable results. In the 50 patients treated with honey, 90 % of burn wounds were rendered sterile within 7 days (Subrahmanyam 1996). In the 50 patients treated with boiled potato peel dressings, persistent infection was noted within 7 days. Of the burn wounds treated with honey, 100 % healed within 15 days as against 50 % in the

wounds treated with boiled potato peel dressings (mean 10.4 vs. 16.2 days).

Cholesterol Metabolism

Hashimoto et al. (2011) reported that rats fed a potato pulp (PP)-supplemented diet for 4 weeks improved both cecal conditions and cholesterol metabolism, suggesting that potato pulp had prebiotic effects. Rats fed with the PP-supplemented diet showed increased cecal ratios of *Lactobacillus* and *Clostridia* and decreased cecal ratios of *Bacteroides* and *Gamma*proteobacteria with slightly negative and positive correlations with plasma T-cholesterol levels, respectively. Mandimika et al. (2008) found that PI3K/AKT, JNK and ERK pathways were not crucial for the induction of cholesterol biosynthesis gene SREBP-2 transcription in intestinal caco-2 epithelial cells following treatment with the potato glycoalkaloid α -chaconine.

Pharmacokinetic Studies

Potato glycoalkaloids, α -solanine and α -chaconine, were detected in all blood serum samples collected from seven volunteers 1–25 h after a meal of potatoes (Hellenäs et al. 1992). Their aglycone, solanidine, was detected in some samples, but there were no traces of the mono- or diglycosides. The average apparent biological half-lives for α -solanine and α -chaconine were 11 and 19 h, respectively. In a randomised, controlled double-blinded, crossover pilot study of three men, consumption of zeaxanthin-rich mashed potatoes significantly increased chylomicron zeaxanthin concentrations suggesting that potentially such potatoes could be used as an important dietary source of zeaxanthin (Bub et al. 2008). There were no significant differences in the concentrations of other major potato carotenoids such as lutein and β -carotene in chylomicrons after consumption of genetically modified and wild-type control potatoes.

Miranda et al. (2013) found that iron uptake, as evaluated by a ferritin assay, by intestinal

human cells was decreased after incubation with the intestinal phase of in-vitro digestion, presumably due to the presence of polyphenols (chlorogenic acid and derivatives and rutin) from potatoes and sweet potatoes.

Trypanocidal Activity

The glycoalkaloids α -chaconine, α -solanine, solasonine, sycophantine and tomatine, as well as the aglycones demissidine, solanidine, solanocapsine, solasodine, tomatidine and veratrine, were tested as growth inhibitors of *Trypanosoma cruzi*, strain EP (Chataing et al. 1998). Glycoalkaloids containing α -chacotriose, namely, α -chaconine, and the aglycone solanidine showed trypanolytic activity against the epimastigote form and trypanocidal activity against the bloodstream and metacyclic trypomastigote form of *Trypanosoma cruzi* in culture medium in micromolar concentrations.

Toxicological Studies

Rabbits fed on greened potatoes became dull and showed reduction in body weight after 30 days of feeding (Azim et al. 1982). They had comparatively enlarged livers and also showed a significant difference in relative size of heart. Blood samples collected from these animals after 30 days showed an increase in the concentration of cholesterol and sugars in blood plasma and a decrease in protein. Plasma electrolytes showed an increase in Ca^{2+} and a decrease in Na^+ and K^+ . There was a decrease in protein content of the liver, kidney, heart and intestine. The glycogen content of liver and kidney was also decreased though glycogen concentration increased in heart tissue. Cholesterol levels were increased in each of these organs. There was a decrease in Ca^{2+} content in the four organs but K^+ content was significantly increased in kidney and intestinal muscles though its concentration was decreased in liver and heart muscles. Na^+ content significantly increased in the heart muscles but decreased in other organs. The results illustrated the toxic nature of the glycoalkaloids in greened potatoes.

Compared to controls, *Solanum elaeagnifolium* and *Solanum dulcamara* fruit, containing appreciable amounts of an unknown spirosolane, an aglycone provisionally identified as soladulcidine, both induced a high percentage incidence of deformed hamster litters with congenital craniofacial malformations (20.4 and 16.3, respectively) that was statistically significant, while percentage incidence of deformed litters induced by *Solanum sarrachoides* and *Solanum melongena* fruit containing mainly solasodine glycosides (9.5 and 7.6 respectively) were both higher than controls (3.4 %), in neither case was the incidence statistically significant (Keeler et al. 1990). Deformed litter incidence induced by sprouts of *Solanum tuberosum*, containing mainly solanidine glycosides, was 24.0 %. Oral administration of the steroidal alkaloid glycosides α -solanine and α -chaconine from potato var. Kennebec sprouts and their aglycone solanidine was shown to induce craniofacial malformations (exencephaly, encephalocele and anophthalmia) in Syrian hamsters (Gaffield and Keeler 1996). Malformation induction was observed in litters upon dosing both the non-toxic aglycone solanidine and the derivative solanidine N-oxide at higher levels. The relatively high teratogenicity of non-toxic solanidine, compared to the glycosides, demonstrated that terata induction by solanidanes was not due to maternal toxicity nor was the oligosaccharide portion of steroidal alkaloid glycosides required to facilitate passage of the teratogen to the foetus.

Aqueous potato leaf extracts containing glycoalkaloids (PGA) (α -solanine and α -chaconine) were cytotoxic to Chinese hamster ovary cells and lysed human, rat and hamster blood cells with no difference in sensitivity among species (Phillips et al. 1996). Oral administration of potato tops to rats, mice and Syrian hamsters had no adverse effects at the highest practicable dose. A mixture of α -solanine and α -chaconine (1:1, w/w) given orally at doses of up to 50 mg/kg body weight to hamsters had no effect, but a single i.p. injection of 25 mg/kg body weight or greater was lethal, with bleeding in the gut. High concentrations of cytotoxic PGA were found in some potato tops, but their effect in laboratory

animals was minimal. The authors concluded that the consumption of moderate quantities of potato tops (2–5 g/kg body weight/day) was unlikely to represent an acute health hazard to humans.

Feeding non-pregnant mice for 14 days on a diet containing 2.4 mmol/kg of aglycone solanidine (derived by hydrolytic removal of the carbohydrate side chain from the potato glycoalkaloids α -chaconine and α -solanine) resulted in significantly greater ratios of % liver weights to body weights (%LW/BWs) 25 than those of the control values (Friedman et al. 2003a). The corresponding increase in pregnant mice was 5.3 for solanidine. For pregnant mice, (a) body weight gain –36.1 for solanidine was less than with control, solanidine; (b) litter weight with solanidine –27.0 was less than control; and (c) the average weight of the foetuses for solanidine –11.2 was less than the control. Abortion of foetuses occurred in five of 24 pregnant mice on the solanidine diet. In vitro assays for estrogenic activity, solanidine at 10- μ M concentration exhibited an increase in the MCF-7 human breast cancer cell proliferation.

In an acute animal toxicity study, daily doses of potato α -solanine (100 mg/kg body weight (BW)) induced death in two of four hamsters within 4 days, when administered by gavage to female Syrian hamsters (Langkilde et al. 2008). Doses of 100 mg of α -chaconine alone or α -solanine and α -chaconine combined in a ratio of 1:2.5, in doses of 75 or 100 mg/kg BW, induced death in one of four hamsters within the same period. Animals dosed with α -solanine alone or in combination with α -chaconine suffered from fluid-filled and dilated small intestines. The glycoalkaloid (GA) administration had no effect on acetylcholinesterase (AChE) or butyrylcholinesterase (BuChE) activity in plasma or the brain. In addition, metabolomics gave direct evidence of glycolytic metabolism of the GA with the β 1, β 2 and γ GAs detected in the urine and, to a lesser extent, the faeces. Doses from 75 mg/kg BW of α -chaconine, α -solanine or the two compounds combined were potentially lethal within 4–5 days in the Syrian Golden hamster. However, the cause of death in these studies could not be established. No synergistic effects of α -solanine combined with α -chaconine were evident. In another study,

doses of up to 33.3-mg total glycoalkaloids/kg body weight were applied in ratios of 1:3.7 and 1:70 (α -solanine/ α -chaconine) to Syrian Golden hamster by gavage for 28 days (Langkilde et al. 2009). Administration of the highest doses of both ratios resulted in distended and fluid-filled small intestines and stomach. Animals receiving the ratio with the reduced content of α -solanine were less affected compared to those receiving the other ratio. In a 90-day feeding trial with the Syrian Golden hamster, administration of 60 % freeze-dried potato powder of a GM potato line (SGT 9–2) with reduced α -solanine content, and the parental control line (Desiree wild type) with a traditional α -solanine/ α -chaconine ratio, did not raise concerns related to nutritional value or safety (Langkilde et al. 2012). Results of the feeding trials showed a low number of significant differences between potato lines with different α -solanine/ α -chaconine ratio, but none were considered to raise safety concerns with regard to human (or animal) consumption.

In a clinical study, human volunteers were administered one of 6 treatments of solutions with TGA (total glycoalkaloid) doses of 0.30, 0.50 or 0.70 mg/kg body weight (bw) or 4–6 mashed potatoes with TGA doses of 0.95, 1.10 or 1.25 mg/kg bw (Mesinga et al. 2005). Mashed potatoes contained TGA level of nearly 200 mg/kg fresh weight (presently recognised as upper limit of safety). The administered single dose of up to 90.2 mg TGA (1.25mgTGA/kg body weight) did not induce acute systemic effects. In one subject at the highest level of exposure (1.25mgTGA/kg body weight), some vomiting was experienced possibly due to local glycoalkaloid toxicity. The results also showed that the clearance of glycoalkaloids took more than 24 h, thus allowing the substance to accumulate in the body. They asserted that additional studies were required to establish an adequate based no observed adverse effect level (NOAEL).

The toxicological monograph produced by the JointFAO/WHO Expert Committee on Food Additives (JECFA) in 1993 stated that glycoalkaloids were not acutely toxic by the oral route in laboratory animals even at very high doses (up to 1 g/kg bodyweight) in some species. The com-

mittee considered that the evidence implicating glycoalkaloids in potato poisoning cases was not convincing. JECFA concluded that levels of α -solanine and α -chaconine normally found in potatoes (20–100 mg/kg) were not of toxicological concern. Nevertheless, JECFA and others have expressed concern about glycoalkaloids in skin-on potato products, such as crisps, that became widely available in the mid-1990s. Glycoalkaloid concentrations of up to 720 mg/kg were found in green-skinned crisps, compared with a maximum of 150 mg/kg in normal crisps.

Freeze-dried potato peel aqueous extract was found to be non-mutagenic using the in-vitro *Salmonella typhimurium*–*Escherichia coli* microsome assay; plate counts revealed <10 CFU/g (De Sotillo et al. 1998). It was effective only at high concentration against Gram-negative and one Gram-positive bacteria but it was bacteriostatic. In the frog embryo teratogenesis assay—*Xenopus* (FETAX), α -chaconine was teratogenic and more embryotoxic than α -solanine; in terms of the median lethal concentration (LC_{50}) after 96 h of exposure, the concentration inducing gross terata in 50 % of the surviving frog embryos (96-h EC_{50} , malformation) and the minimum concentration needed to inhibit the growth of frog embryos (Friedman et al. 1991). The aglycones demissidine, solanidine and solasodine were less toxic than the glycosides α -chaconine and α -solanine.

The glycol-alkaloid extracts were also reported active against *Microsporium gypseum* and *Cryptococcus neoformans*, *Artemia salina* nauplii and *Trypanosoma cruzi* and showed intra-peritoneal subacute toxicity in mice.

Adverse Toxicity Issues

The total glycoalkaloid content (TGA) of potato tubers had been reported to vary widely; values between 2 and 410 mg/100 g of fresh weight (FW) had been reported (Lisinska and Leszczynski 1989), but in most cases the TGA concentration in whole tubers was between 10 and 150 mg/100 g of FW (Gelder et al. 1988). Cooking and frying had been reported to not

destroy the glycoalkaloids (Maga 1994). The widely accepted safety limit for the level of total glycoalkaloids (TGA) in tubers was stated as 200 mg/kg of FW (Boemer and Mattis 1924; Smith et al. 1996). Mild clinical symptoms of glycoalkaloid poisoning include abdominal pain, vomiting and diarrhoea (Friedman and McDonald 1997). Severe glycoalkaloid poisoning caused symptoms ranging from gastrointestinal disorders through confusion, hallucination and partial paralysis to convulsions, coma and death (Smith et al. 1996). Evidence suggested that human susceptibility to glycoalkaloid poisoning was high and very variable: oral doses in the range of 1–5 mg/kg of body weight were marginally to severely toxic to humans (Hellenäs et al. 1992, whereas 3–6 mg/kg of body weight could be lethal (Morris and Lee 1984). Glycoalkaloids (α -solanine and α -chaconine) had been reported to contribute flavour to potatoes but at higher concentrations (>200 mg/kg) caused bitterness (Friedman 2006) and were toxic to humans (Ostrý et al. 2010). α -Solanine and α -chaconine appeared to have two main toxic actions, one on disruption of cell membranes (Roddick et al. 1990; Keukens et al. 1992, 1995, 1996) and another one on acetylcholinesterase (Huxtable 1992). Symptoms of α -solanine/ α -chaconine poisoning involve an acute gastrointestinal upset with diarrhoea, vomiting and severe abdominal pain (Friedman 2006). The steroidal glycoalkaloid solamargine caused significant disruption of phosphatidylcholine/cholesterol liposomes at a concentration >50 μ M, whereas the normally co-occurring glycoalkaloid solasonine was ineffective at up to 150 μ M (Roddick et al. 1990). In combination, the two compounds produced a marked synergism. Synergistic effects were also observed with certain combinations of these and potato glycoalkaloids, viz. solamargine and solanine and also solasonine and chaconine.

Keukens et al. (1992) found that glycoalkaloids α -solanine, α -chaconine, α -tomatine and the aglycone solanidine were able to interact strongly with sterol containing membranes, thereby causing membrane disruption. The order of potency of the glycoalkaloids was α -tomatine > α -chaconine > α -solanine. The plant sterols

β -sitosterol and fucosterol showed higher affinity for glycoalkaloids as compared to cholesterol and ergosterol. The mode of action of the glycoalkaloids was proposed to consist of three main steps: (1) insertion of the aglycone part in the bilayer, (2) complex formation of the glycoalkaloid with the sterols present and (3) rearrangement of the membrane caused by the formation of a network of sterol–glycoalkaloid complexes resulting in a transient disruption of the bilayer leading to leakage. They found that the most important properties for sterols to interact with glycoalkaloids turned out to be a planar ring structure and a 3 β -OH group, whereas for α -chaconine the 5–6 double bonds and the 10-methyl group were also of importance. The importance of sugar–sugar interactions was illustrated by the high synergistic effect between α -chaconine and α -solanine, the leakage enhancing effect of glycolipids and the almost complete loss of activity after deleting one or more monosaccharides from the glycoalkaloids (Keukens et al. 1995). They further found that these glycoalkaloids specifically induced membrane disruptive effects of cholesterol-containing membranes as was previously reported in model membrane studies (Keukens et al. 1996). In addition, α -chaconine was found to selectively decrease gap-junctional intercellular communication. Furthermore, the glycoalkaloids were more potent in permeabilising the outer membrane of mitochondria compared to digitonin at the low concentrations used.

Studies by Friedman et al. (1996) found that feeding of potato, tomato and eggplant alkaloids affected food consumption and body and liver weights in mice. The relative liver weights (liver weight/body weight \times 100, %LW/BW) were lower than that of controls in mice fed the potato glycoalkaloid α -chaconine (–10 %) for 7 days with the 2.4 mmol/kg diet dose. Under these same conditions, %LW/BW was greater than that of controls in mice fed two aglycones: solanidine (27 %) and solasodine (8 %). Relative liver weight increases induced by the aglycones were determined under time and dose conditions in which differences in body weight and food consumption were not significant (2.4 mmol/kg diet

for 28 days). Under these conditions, the observed %LW/BW increases relative to the controls were as follows: solanidine (32 %), solasodine (22 %) and dehydroepiandrosterone (DHEA) (16 %). Solanidine, solasodine and DHEA were equally potent and were more potent than tomatidine. Storage of potatoes at 5 °C increased the proportions of the 4-*O*- α -D-galactoside of calystegine B₂ and the trihydroxylated calystegine A₃ (Watson et al. 2000). Mice treated with calystegine A₃ showed vacuolation of Kupffer cells with minimal vacuolation in other histiocytic cells. The microflora in rumen fluid removed from sheep previously fed hay reduced calystegines B₁ and B₂ to undetectable levels, but the concentrations of calystegine A₃ and the control compound swainsonine were not affected. There was no effect on the overall respiratory rate of the microbial population by any of these alkaloids.

Exposure of T84 cultured intestinal epithelial monolayers to potato glycoalkaloids (solanine and chaconine) permeabilised the cholesterol-containing membranes, with chaconine/solanine 1:1 mixture > chaconine > solanine, and led to the disruption of epithelial barrier integrity in a concentration-dependent fashion (Patel et al. 2002). In-vivo oral feeding experiments demonstrated that chaconine/solanine ingestion, at physiologic concentrations, aggravated histologic colonic injury in mice genetically predisposed to developing inflammatory bowel disease (IBD). Iablokov et al. (2010) demonstrated that consumption of deep-fried potato skins containing glycoalkaloids by interleukin 10 gene-deficient mice significantly elevated levels of ileal interferon IFN- γ relative to controls. Mice in the dextran sodium sulphate colitis IBD model that were fed the same strain of potatoes demonstrated significantly elevated levels of pro-inflammatory cytokines IFN- γ , TNF- α and IL-17 in the colon in addition to an enhanced colonic permeability. They concluded that consumption of potato skins containing glycoalkaloids could significantly aggravate intestinal inflammation in predisposed individuals.

Studies by Wang et al. (2005) concluded that exposure of bovine oocytes to potato steroidal

glycoalkaloids (α -solanine and α -chaconine) during in-vitro maturation inhibited subsequent pre-implantation embryo development. This effect was significant during the later pre-implantation embryo development period as indicated by fewer numbers of expanded and hatched blastocysts produced in the media containing these alkaloids. They suggested that ingestion of *Solanum* species containing toxic amounts of glycoalkaloids may have negative effects on pre-implantation embryonic survival.

Hansen (1925) reported the fatal case of two members of a family of seven after a cooked meal of greened potatoes, and symptoms sustained included extreme exhaustion, restlessness, rapid breathing and loss of consciousness; the loss of six pigs due to eating sprouted, uncooked potatoes and the death of 30 chickens that died after consuming a large quantity of green potato sprouts. He also cited Macfayden who demonstrated that old sprouted potatoes were poisonous to horses. McMillan and Thompson (1979) reported an outbreak of suspected solanine poisoning in 78 schoolboys who became ill after eating cooked old potato at lunch. They suffered from diarrhoea, vomiting and circulatory, neurological and dermatological problems, with 17 of the boys being hospitalised. The amount of solanine in potato waste recovered after the meal was excessive as assessed by its anticholinesterase activity. The amount of α -solanine and α -chaconine in the flesh and peel of potatoes from a bag known to have been left from the previous term was high. Hellenäs et al. (1995a) reported that in Sweden, there were no indications of serious or widespread adverse health effects in consumers consuming potatoes with high glycoalkaloid levels, although there was circumstantial evidence that a few cases of temporary gastrointestinal disturbances were caused by consumption of Magnum Bonum potatoes with glycoalkaloid concentrations in the range 310–1000 mg/kg.

Traditional Medicinal Uses

Fomentations of potato juice followed by an application of liniment and ointment have been employed to relieve acute pain in cases of gout,

rheumatism and lumbago (Grieve 1971). Sprains and bruises have also been successfully treated by the potato-juice preparations, and in cases of synovitis rapid absorption of the fluid has resulted. Hot potato water has in years past been a popular remedy for some forms of rheumatism, fomentations to swollen and painful parts, as hot as can be borne. Uncooked, peeled potatoes, pounded in a mortar and applied cold, have been found to make a very soothing plaster to parts that have been scalded or burnt. The mealy flour of baked potato, mixed with sweet oil, is a very healing application for frostbites. In Derbyshire, hot boiled potatoes are used for corns. In Rwanda, potato tuber and carrot are pounded and the extract taken orally to treat dyspepsia and as a laxative (Kayonga and Habiwaremye 1987). In Ethiopia, the leaf extract is used against bacteria species causing tonsillitis (Desta 1993). In Morocco, a slice of potato is used to treat bruises, sprain and blisters and a poultice of potato used to treat fever and sunstroke (Bellakhdar 1997). In Cameroon, a mixture of potato tuber, avocado and honey is used as a poultice topically for injuries and wounds, and a decoction of carrot, potato tuber, orange fruit and green clay and honey is taken orally for cough, asthma and sinusitis (Nnomo et al. 2009).

Other Uses

The tubers are also used as animal feed in parts of Eastern Europe. Potato starch is used in the textile, cosmetic, pharmaceutical and paper industries and in the production of derived substances such as ethanol glucose (Graves 2001).

Both the potato peel waste and PPW fermentation residue had shown potential based on properties to be converted into crude biofuel via thermochemical processes (Liang and McDonald 2014).

Although young potatoes contain no citric acid, the mature tubers yield enough even for commercial purposes, and ripe potato juice is an excellent cleaner of silks, cottons and woollens (Grieve 1971).

In pure form, both potato glycoalkaloids, α -solanine and α -chaconine, deterred snail (*Helix aspersa*) feeding, with chaconine being the more active compound (Smith et al. 2001). In combination, authentic solanine and chaconine interacted synergistically in their inhibition of feeding. Comparison of data from peel extracts of all three potato varieties and authentic glycoalkaloids indicated that the level of feeding inhibition by the extracts was, at least in part, a consequence of a synergism between solanine and chaconine.

Studies by Okeke and Frankenberger (2005) found that potato peel waste in combination with amylolytic microorganisms (*Citrobacter* sp. S4, *Streptomyces* sp. S2, *Flavobacterium* sp. S6, *Pseudoxanthomonas* sp. S5, *Streptomyces* sp. S7 and *Aeromonas* sp. S8) and *Dechlorosoma* sp. could be economically used to achieve complete perchlorate removal from water.

Comments

The leading potato-producing countries in the world based on 2013 production (tonnes) (FAOSTAT 2014) are China, 88,925,000; India, 45,343,600; Russian Federation, 30,199,126; Ukraine, 22,258,600; USA, 9,843,919; Germany, 9,669,700; Bangladesh, 8,603,000; France, 6,975,000; Netherlands, 6,801,000; Poland, 6,334,200; United Kingdom, 5,580,000; and Iran, 5,560,000.

Selected References

- Albishi T, John JA, Al-Khalifa AS, Shahidi F (2013) Phenolic content and antioxidant activities of selected potato varieties and their processing by-products. *J Funct Foods* 5(2):590–600
- Al-Saikhhan MS, Howard LR, Miller JC Jr (1995) Antioxidant activity and total phenolics in different genotypes of potato (*Solanum tuberosum* L.). *J Food Sci* 60:341–343
- Alvani K, Qi X, Tester RF, Snape CE (2011) Physico-chemical properties of potato starches. *Food Chem* 125(3):958–965
- Amado IR, Franco D, Sánchez M, Zapata C, Vázquez JA (2014) Optimisation of antioxidant extraction from *Solanum tuberosum* potato peel waste by surface response methodology. *Food Chem* 165:290–299
- Andre CM, Ghislain M, Bertin P, Oufir M, Herrera Mdel R, Hoffmann L, Hausman JF, Larondelle Y, Evers D (2007a) Andean potato cultivars (*Solanum tuberosum* L.) as a source of antioxidant and mineral micronutrients. *J Agric Food Chem* 55(2):366–378
- Andre CM, Oufir M, Guignard C, Hoffmann L, Hausman J-F, Evers D, Larondelle Y (2007b) Antioxidant profiling of native andean potato tubers (*Solanum tuberosum* L.) reveals cultivars with high levels of β -carotene, α -tocopherol, chlorogenic acid, and petanin. *J Agric Food Chem* 55(26):10839–10849
- Andre CM, Schafleitner R, Guignard C, Oufir M, Aliaga CA, Nomberto G, Hoffmann L, Hausman JF, Evers D, Larondelle Y (2009) Modification of the health-promoting value of potato tubers field grown under drought stress: emphasis on dietary antioxidant and glycoalkaloid contents in five native andean cultivars (*Solanum tuberosum* L.). *J Agric Food Chem* 57(2):599–609
- Andrews DL, Beames B, Summers MD, Park WD (1988) Characterization of the lipid acyl hydrolase activity of the major potato (*Solanum tuberosum*) tuber protein, patatin, by cloning and abundant expression in a baculovirus vector. *Biochem J* 252(1):199–206
- Anstis PJP, Northcote DH (1975) Cytokinin activity in potato tuber extracts. *Z Pflanzenphysiol* 75(3):273–275
- Arab A, Trigo JR, Lourenção AL, Peixoto AM, Ramos F, Bento JM (2007) Differential attractiveness of potato tuber volatiles to *Phthorimaea operculella* (Gelechiidae) and the predator *Orius insidiosus* (Anthocoridae). *J Chem Ecol* 33(10):1845–1855
- Ardenne M, Steinfelder K, Tummler R, Schreiber K (1963) Molekul-massenspektrographie von naturstoffen. 1. Mitteilung: steroide. *Experientia* 19:178–180
- Ardenne M, Osske G, Schreiber K, Steinfelder K, Tummler R (1965) Sterine und Triterpenoide. X. Über die sterine des kartoffelkäfers, *Leptinotarsa decemlineata* Say. *J Insect Physiol* 11(10):1365–1376
- Arrieta-Baez D, Stark RE (2006) Using trifluoroacetic acid to augment studies of potato suberin molecular structure. *J Agric Food Chem* 54(26):9636–9641
- Asano N, Kato A, Matsui K, Watson AA, Nash RJ, Molyneux RJ, Hackett L, Topping J, Winchester B (1997) The effects of calystegines isolated from edible fruits and vegetables on mammalian liver glycosidases. *Glycobiology* 7(8):1085–1088
- Attoumbré J, Lesur D, Giordanengo P, Baltora-Rosset S (2012) Preparative separation of glycoalkaloids α -solanine and α -chaconine by centrifugal partition chromatography. *J Chromatogr B Analyt Technol Biomed Life Sci* 908:150–154
- Attoumbré J, Giordanengo P, Baltora-Rosset S (2013) Solanidine isolation from *Solanum tuberosum* by centrifugal partition chromatography. *J Sep Sci* 36(14):2379–2385
- Azim A, Shaikh HA, Ahmad R (1982) Effect of feeding greened potatoes on different visceral organs and blood plasma of rabbits. *J Sci Food Agric* 33(12):1275–1279

- Aziz A, Randhawa MA, Butt MS, Asghar A, Yasin M, Shibamoto T (2012) Glycoalkaloids (α -chaconine and α -solanine) contents of selected Pakistani potato cultivars and their dietary intake assessment. *J Food Sci* 77(3):T58–T61
- Bártová V, Bárta J (2009) Chemical composition and nutritional value of protein concentrates isolated from potato (*Solanum tuberosum* L.) fruit juice by precipitation with ethanol or ferric chloride. *J Agric Food Chem* 57(19):9028–9034
- Baup M (1826) Extrait d'une lettre sur plusieurs nouvelles substances. *Ann Chim Phys* 31:108–109
- Bellakhdar J (1997) La pharmacopée marocaine traditionnelle: Médecine arabe ancienne et savoirs populaires. Ibis Press, Paris, 764 pp. (in French)
- Bergenstråhle A, Tillberg E, Jonsson L (1992) Regulation of glycoalkaloid accumulation in potato tuber disks. *J Plant Physiol* 140(3):269–275
- Bergenstråhle A, Borga P, Jonsson MV (1996) Sterol composition and synthesis in potato tuber discs in relation to glycoalkaloid synthesis. *Phytochemistry* 41:155–161
- Bernards MA, Razem FA (2001) The poly(phenolic) domain of potato suberin: a non-lignin cell wall biopolymer. *Phytochemistry* 57(7):1115–1122
- Bethke PC, Bussan AJ (2013) Acrylamide in processed potato products. *Am J Potato Res* 90(5):403–424
- Blanda G, Cerretani L, Comandini P, Toschi TG, Lercker G (2010) Investigation of off-odour and off-flavour development in boiled potatoes. *Food Chem* 118(2):283–290
- Blasiole S, Biondi E, Samudrala D, Spinelli F, Cellini A, Bertaccini A, Cristescu SM, Braschi I (2014) Identification of volatile markers in potato brown rot and ring rot by combined GC-MS and PTR-MS techniques: study on in vitro and in vivo samples. *J Agric Food Chem* 62:337–347
- Boemer A, Mattis H (1924) Der solaniningehalt der kartoffeln. *Z Unters Nahr Genussm Gebrauchs-gegenstaende* 47:97–127
- Bolter CJ, Dicke M, Van Loon JJ, Visser JH, Posthumus MA (1997) Attraction of Colorado potato beetle to herbivore-damaged plants during herbivory and after its termination. *J Chem Ecol* 23(4):1003–1023
- Breithaupt DE, Bamedi A (2002) Carotenoids and carotenoid esters in potatoes (*Solanum tuberosum* L.): new insights into an ancient vegetable. *J Agric Food Chem* 50(24):7175–7181
- Bretzlöff CW (1971) A method for the rapid estimation of glycoalkaloids in potato tubers. *Am Potato J* 48(5):158–162
- Brown CR (2005) Antioxidants in potato. *Am J Potato Res* 82(2):163–172
- Brown CR (2006) Anthocyanin and carotenoid contents in potato: breeding for the specialty market. *Proc Idaho Winter Commod Schools* 39:157–163
- Brown CR, Wrolstad R, Durst R, Yang C-P, Clevidence BA (2003) Breeding studies in potatoes containing high concentrations of anthocyanins. *Am J Potato Res* 80:241–249
- Brown CR, Culley D, Bonierbale M, Amorós W (2007) Anthocyanin, carotenoid content, and antioxidant values in native South American potato cultivars. *HortScience* 42(7):1733–1736
- Brown CR, Durst RW, Wrolstad R, De Jong W (2008) Variability of phytonutrient content of potato in relation to growing location and cooking method. *Potato Res* 51(3–4):259–270
- Bub A, Möseneder J, Wenzel G, Rechkemmer G, Briviba K (2008) Zeaxanthin is bioavailable from genetically modified zeaxanthin-rich potatoes. *Eur J Nutr* 47(2):99–103
- Burgos G, Muñoz L, Sosa P, Bonierbale M, zum Felde T, Díaz C (2013) In vitro bioaccessibility of lutein and zeaxanthin of yellow fleshed boiled potatoes. *Plant Foods Hum Nutr* 68(4):385–390
- Burton WG, Meigh DF (1971) The production of growth-suppressing volatile substances by stored potato tubers. *Potato Res* 14(2):96–101
- Bushway RJ, Ponnampalam R (1981) α -Chaconine and α -solanine content of potato products and their stability during several modes of cooking. *Agric Food Chem* 29(4):814–817
- Bushway RJ, Bureau JL, McGann DF (1983) Alpha-chaconine and alpha-solanine content of potato peels and potato peel products. *J Food Sci* 48:84–86
- Buttery RG (1973) Unusual volatile carbonyl components of potato chips. *J Agric Food Chem* 21(1):31–33
- Buttery RG, Ling LC (1972) Characterization of nonbasic steam volatile components of potato chips. *J Agric Food Chem* 20(3):698–700
- Buttery RG, Ling LC (1973) Earthy aroma of potatoes. *J Agric Food Chem* 21(4):745–746
- Buttery RG, Seifert RM, Ling LC (1970) Characterization of some volatile potato components. *J Agric Food Chem* 18(3):538–539
- Buttery RG, Seifert RM, Guadagni DG, Ling LC (1971) Characterization of volatile pyrazine and pyridine components of potato chips. *J Agric Food Chem* 19(5):969–971
- Buttery RG, Guadagni DG, Ling LC (1973) Volatile components of baked potatoes. *J Sci Food Agric* 24:1125–1131
- Cahill MG, Caprioli G, Vittori S, James KJ (2010) Elucidation of the mass fragmentation pathways of potato glycoalkaloids and aglycons using Orbitrap mass spectrometry. *J Mass Spectrom* 45(9):1019–1025
- Carlin JT, Jin QZ, Huang TC, Ho CT, Chang SS (1986) Identification of alkylloxazoles in the volatile compounds from French-fried potatoes. *J Agric Food Chem* 34(4):621–623
- Carlin JT, Ho CT, Chang SS, Velluz A, Pickenhagen W (1990) Analysis of French fried potato flavor: identification of 3-(methylthio) alkanals. *Lebensm Wiss Technol* 23(3):276
- Castro G, Kraus T, Abdala G (1999) Endogenous jasmonic acid and radial cell expansion in buds of potato tubers. *J Plant Physiol* 155(6):706–710

- Chataing B, Concepcion JL, Lobaton R, Usubillaga A (1998) Inhibition of *Trypanosoma cruzi* growth *in vitro* by Solanum alkaloids: a comparison with ketoconazole. *Planta Med* 64(1):31–36
- Chiou A, Salta FN, Kalogeropoulos N, Mylona A, Ntalla I, Andrikopoulos NK (2007) Retention and distribution of polyphenols after pan-frying of French fries in oils enriched with olive leaf extract. *J. Food Sci* 72(8):S574–S584
- Chiou A, Kalogeropoulos N, Salta FN, Efstathiou P, Andrikopoulos NK (2009) Pan-frying of French fries in three different edible oils enriched with olive leaf extract: oxidative stability and fate of microconstituents. *LWT-Food Sci Technol* 42(6):1090–1097
- Chong ES, McGhie TK, Heyes JA, Stowell KM (2013) Metabolite profiling and quantification of phytochemicals in potato extracts using ultra-high-performance liquid chromatography-mass spectrometry. *J Sci Food Agric* 93(15):3801–3808
- Coleman EC, Ho CT (1980) Chemistry of baked potato flavor. 1. Pyrazines and thiazoles identified in the volatile flavor of baked potato. *J Agric Food Chem* 28(1):66–68
- Coleman EC, Ho CT, Chang SS (1981) Isolation and identification of volatile compounds from baked potatoes. *J Agric Food Chem* 29(1):42–48
- Coquoz JL, Buchala A, Métraux JP (1998) The biosynthesis of salicylic acid in potato plants. *Plant Physiol* 117(3):1095–1101
- Creech DL, Workman M, Harrison MD (1973) The influence of storage factors on endogenous ethylene production by potato tubers. *Am Potato J* 50(5):145–150
- Cummings JH, Bingham SA, Heaton KW, Eastwood MA (1992) Fecal weight, colon cancer risk, and dietary intake of nonstarch polysaccharides (dietary fiber). *Gastroenterology* 103:1783–1789
- Curl AL, Nelson EK (1940) The non-volatile acids of the potato. *Am Potato J* 17(12):328–330
- Dale MFB, Mackay GR (1994) Inheritance of table and processing quality. In: Bradshaw JE, Mackay GR (eds) *Potato genetics*. CAB International, Wallingford, pp 285–315
- Dattatreya RM, Nuijen S, van Swaaij AC, Kloppe PJ (1991) Evaluation of boiled potato peel as a wound dressing. *Burns* 17(4):323–328
- Davies AMC, Blincow PJ (1984) Glycoalkaloid content of potatoes and potato products sold in the UK. *J Sci Food Agric* 35(5):553–557
- De Lacy Costello B, Evans P, Ewen R, Gunson H, Ratcliffe NM, Spencer-Phillips PT (1999) Identification of volatiles generated by potato tubers (*Solanum tuberosum* CV: Maris Piper) infected by *Erwinia carotovora*, *Bacillus polymyxa* and *Arthrobacter* sp. *Plant Pathol* 48(3):345–351
- De Lacy Costello BPJ, Evans P, Ewen RJ, Gunson HE, Jones PRH, Ratcliffe NM, Spencer-Phillips PTN (2001) Gas chromatography–mass spectrometry analyses of volatile organic compounds from potato tubers inoculated with *Phytophthora infestans* or *Fusarium coeruleum*. *Plant Pathol* 50(4):489–496
- De Lorenzo MS, Menna PL, Alonso DF, Gomez E (2001) *In vitro* activity of a *Solanum tuberosum* extract against mammary carcinoma cells. *Planta Med* 67:164–166
- De Sotillo DR, Hadley M, Holm ET (1994a) Phenolics in aqueous potato peel extract: extraction, identification and degradation. *J Food Sci* 59(3):649–651
- De Sotillo DR, Hadley M, Holm ET (1994b) Potato peel waste: stability and antioxidant activity of a freeze-dried extract. *J Food Sci* 59(5):1031–1033
- De Sotillo DR, Hadley M, Wolf-Hall C (1998) Potato peel extract a nonmutagenic antioxidant with potential antimicrobial activity. *J Food Sci* 63(5):907–910
- Deck RE, Chang SS (1965) Identification of 2,5-dimethylpyrazine in the volatile flavour compounds of potato chips. *Chem Ind (London)* 30:1343–1344
- Deck RE, Pokorny J, Chang SS (1973) Isolation and identification of volatile compounds from potato chips. *J Food Sci* 38(2):345–349
- Del Mar Verde Méndez C, Rodríguez Delgado MÁ, Rodríguez Rodríguez EM, Díaz Romero C (2004) Content of free phenolic compounds in cultivars of potatoes harvested in Tenerife (Canary Islands). *J Agric Food Chem* 52(5):1323–1327
- Delgado JA, Schwarz PB, Gillespie J, Rivera-Varas VV, Secor GA (2010) Trichothecene mycotoxins associated with potato dry rot caused by *Fusarium graminearum*. *Phytopathology* 100(3):290–296
- Desborough S, Peloquin SJ (1966) Disc electrophoresis of tuber proteins from *Solanum* species and interspecific hybrids. *Phytochemistry* 5:727–733
- Desta B (1993) Ethiopian traditional herbal drugs. Part II: antimicrobial activity of 63 medicinal plants. *J Ethnopharmacol* 39(2):129–139
- Deusser H, Guignard C, Hoffmann L, Evers D (2012) Polyphenol and glycoalkaloid contents in potato cultivars grown in Luxembourg. *Food Chem* 135(4):2814–2824
- Dobson G, Griffiths DW, Davies HV, McNicol JW (2004) Comparison of fatty acid and polar lipid contents of tubers from two potato species, *Solanum tuberosum* and *Solanum phureja*. *J Agric Food Chem* 52(20):6306–6314
- Dornseifer TP, Powers JJ (1965) Volatile constituents of potato chips and changes during storage. *Food Technol* 19:877–879
- Dresow JF, Böhm H (2009) The influence of volatile compounds of the flavour of raw, boiled and baked potatoes: Impact of agricultural measures on the volatile components. *Landbauforsch* 4(59):309–338
- Duckham SC, Dodson AT, Bakker J, Ames JM (2001) Volatile flavour components of baked potato flesh. A comparison of eleven potato cultivars. *Nahrung* 45(5):317–323
- Duckham SC, Dodson AT, Bakker J, Ames JM (2002) Effect of cultivar and storage time on the volatile flavor components of baked potato. *J Agric Food Chem* 50(20):5640–5648

- Eichhorn S, Winterhalter P (2005) Anthocyanins from pigmented potato (*Solanum tuberosum* L.) varieties. *Food Res Int* 38(8–9):943–948
- Ek KL, Wang S, Copeland L, Brand-Miller JC (2014) Discovery of a low-glycaemic index potato and relationship with starch digestion in vitro. *Br J Nutr* 111(4):699–705
- Ellner FM (2002) Mycotoxins in potato tubers infected by *Fusarium sambucinum*. *Mycotoxin Res* 18(2):57–61
- Engelbrecht L, Bielinska-Czarnecka M (1972) Increase of cytokinin activity in potato tubers near the end of dormancy. *Biochem Physiol Pflanz* 163:499–504
- Englyst HN, Kingman SM, Cummings JH (1992) Classification and measurement of nutritionally important starch fractions. *Eur J Clin Nutr* 46(suppl 2):S33–S50
- Espelie KE, Sadek NZ, Kolattukudy PE (1980) Composition of suberin-associated waxes from the subterranean storage organs of seven plants. *Planta* 148(5):468–476
- Ezekiel R, Rana G, Singh N, Singh S (2007) Physicochemical, thermal and pasting properties of starch separated from γ -irradiated and stored potatoes. *Food Chem* 105(4):1420–1429
- Ezekiel R, Rana G, Singh N, Singh S (2010) Physicochemical and pasting properties of starch from stored potato tubers. *J Food Sci Technol* 47(2):195–201
- Ezekiel R, Singh N, Sharma S, Kaur A (2013) Beneficial phytochemicals in potato—a review. *Food Res Int* 50(2):487–496
- Faivre J, Boutron MC, Quipourt V (1993) Diet and large bowel cancer. In: Zappia V (ed) *Advances in nutrition and cancer*. Plenum Press, New York, pp 107–118
- FAO (2014) FAO STAT. Food and Agricultural Organization of United Nations: Economic And Social Department: The Statistical Division. <http://faostat.fao.org/site/567/DesktopDefault.aspx?PageID=567>
- Fernandes G, Velangi A, Wolever TM (2005) Glycemic index of potatoes commonly consumed in North America. *J Am Diet Assoc* 105(4):557–562
- Fernandez-Orozco R, Gallardo-Guerrero L, Hornero-Méndez D (2013) Carotenoid profiling in tubers of different potato (*Solanum* sp) cultivars: accumulation of carotenoids mediated by xanthophyll esterification. *Food Chem* 141(3):2864–2872
- Filmer AAE, Rhodes MJC (1984) An assessment of 1, 4, 6-trimethylnaphthalene as a sprout suppressant for stored potato tubers. *Potato Res* 27(4):383–392
- Filmer AAE, Rhodes MJC (1985) Investigation of sprout-growth-inhibitory compounds in the volatile fraction of potato tubers. *Potato Res* 28(3):361–377
- Fischer J (1991) Untersuchungen über flüchtige Aromastoffe der Kartoffel. II. Der Einfluss differenzierter Nährstoffgaben auf das Spektrum der Aromastoffe in Kartoffeln. (Studies on the volatile aromatics in potato. II. The effect of nutrient input on the aromatic spectrum of potato). *Potato Res* 34:169–178
- Fitzpatrick TJ, Herb SF, Osman SF, McDermott JA (1977) Potato glycoalkaloids: increases and variations of ratios in aged slices over prolonged storage. *Am Potato J* 54(11):539–544
- Foot RJ, Haase NU, Grob K, Gondé P (2007) Acrylamide in fried and roasted potato products: a review on progress in mitigation. *Food Addit Contam* 24(Suppl 1):37–46
- Fossen T, Øvstedal DO, Slimestad R, Andersen ØM (2003) Anthocyanins from a Norwegian potato cultivar. *Food Chem* 81(3):433–437
- Freedman MR, Keast DR (2011) White potatoes, including french fries, contribute shortfall nutrients to children's and adolescents' diets. *Nutr Res* 31(4):270–277
- Freedman MR, Keast DR (2012) Potatoes, including French fries, contribute key nutrients to diets of US adults: NHANES 2003–2006. *J Nutr Therap* 1(1):1–11
- Friedman M (2006) Potato glycoalkaloids and metabolites: roles in the plant and in the diet. *J Agric Food Chem* 54:8655–8681
- Friedman M, Dao L (1992) Distribution of glycoalkaloids in potato plants and commercial potato products. *Agric Food Chem* 40(3):419–423
- Friedman M, McDonald GM (1997) Potato glycoalkaloids: chemistry, analysis, safety, and plant physiology. *Crit Rev Plant Sci* 16:55–132
- Friedman M, Rayburn JR, Bantle JA (1991) Developmental toxicology of potato alkaloids in the frog embryo teratogenesis assay - *Xenopus* (FETAX). *Food Chem Toxicol* 29(8):537–547
- Friedman M, Henika PR, Mackey BE (1996) Feeding of potato, tomato and eggplant alkaloids affects food consumption and body and liver weights in mice. *J Nutr* 126(4):989–999
- Friedman M, Henika PR, Mackey BE (2003a) Effect of feeding solanidine, solasodine and tomatidine to non-pregnant and pregnant mice. *Food Chem Toxicol* 41(1):61–71
- Friedman M, Roitman JN, Kozukue N (2003b) Glycoalkaloid and calystegine contents of eight potato cultivars. *J Agric Food Chem* 51(10):2964–2973
- Friedman M, Lee KR, Kim HJ, Lee IS, Kozukue N (2005) Anticarcinogenic effects of glycoalkaloids from potatoes against human cervical, liver, lymphoma, and stomach cancer cells. *J Agric Food Chem* 53(15):6162–6169
- FSANZ (2014) Acrylamide and food. <http://www.food-standards.gov.au/consumer/chemicals/acrylamide/Pages/default.aspx>
- Funayama S, Yoshida K, Konno C, Hikino H (1980) Structure of kukoamine A, a hypotensive principle of *Lycium chinense* root barks. *Tetrahedron Lett* 21(14):1355–1356
- Gaffield W, Keeler RF (1996) Induction of terata in hamsters by solanidine alkaloids derived from *Solanum tuberosum*. *Chem Res Toxicol* 9(2):426–433

- Gao XQ, Yang Q, Minami C, Matsuura H, Kimura A (2003) Inhibitory effect of salicylhydroxamic acid on theobroxide-induced potato tuber formation. *Plant Sci* 165(5):993–999
- Gao SY, Wang QJ, Ji YB (2006) Effect of solanine on the membrane potential of mitochondria in HepG2 cells and $(Ca^{2+})_i$ in the cells. *World J Gastroenterol* 12(21):3359–3367
- García-Alonso A, Goñi I (2000) Effect of processing on potato starch: in vitro availability and glycaemic index. *Nahrung* 44(1):19–22
- Gibson S, Kurilich AC (2013) The nutritional value of potatoes and potato products in the UK diet. *Nutr Bull* 38(4):389–399
- Gilbert GA, Patrick AD (1952a) Enzymes of the potato concerned in the synthesis of starch. I. The separation and crystallization of Q-enzyme. *Biochem J* 51(2):181–186
- Gilbert GA, Patrick AD (1952b) Enzymes of the potato concerned in the synthesis of starch. 2. The separation of phosphorylase. *Biochem J* 51(2):186–190
- Giusti MM, Maria Fernanda Polit MF, Huseyin Ayvaz H, David Tay D, Manrique I (2014) Characterization and quantitation of anthocyanins and other phenolics in native Andean potatoes. *J Agric Food Chem* 62(19):4408–4416
- Gomez-Roldan V, Feras S, Brewer PB, Puech-Pagès V, Dun EA, Jean-Paul Pillot J-P, Fabien Letisse F, Matusova R, Danoun S, Portais J-C, Bouwmeester H, Bécard G, Beveridge CA, Rameau C, Rochange SF (2008) Strigolactone inhibition of shoot branching. *Nature* 455:189–194
- Gorinstein S, Yamagata S, Hadziyev D (1988) Electrophoretic separation of proteins and their amino acid composition in raw and processed potatoes. *J Food Biochem* 12(1):37–50
- Graves C (2001) The potato treasure of the Andes: from agriculture to culture. Int Potato Center (CIP), Lima
- Grieve M (1971) A modern herbal. vols 2, Penguin. Dover Publications, New York, 919 pp
- Griffiths DW, Shepherd T, Stewart D (2008) Comparison of the calyptegine composition and content of potato sprouts and tubers from *Solanum tuberosum* Group Phureja and *Solanum tuberosum* Group Tuberosum. *J Agric Food Chem* 56(13):5197–5204
- Groot EH, Janssen LW, Kentie A, Oosterhuis HK, Trap AJL (1947) A new protein in potatoes. *BiochimBiophys Acta* 1:410–414
- Guadagni DG, Buttery RG, Seifert RM, Venstrom DW (1971) Flavor enhancement of potato products. *J Food Sci* 36(3):363–366
- Guadagni DG, Buttery RG, Turnbaugh JG (1972) Odour thresholds and similarity ratings of some potato chip components. *J Sci Food Agric* 23(12):1435–1444
- Halford NG, Muttucumaru N, Powers SJ, Gillatt PN, Hartley L, Elmore JS, Mottram DS (2012) Concentrations of free amino acids and sugars in nine potato varieties: effects of storage and relationship with acrylamide formation. *J Agric Food Chem* 60:12044–12055
- Han KH, Hashimoto N, Hashimoto M, Noda T, Shimada K, Lee CH, Sekikawa M, Fukushima M (2006a) Red potato extract protects from D-galactosamine-induced liver injury in rats. *Biosci Biotechnol Biochem* 70(9):2285–2288
- Han KH, Sekikawa M, Shimada K, Hashimoto M, Hashimoto N, Noda T, Tanaka H, Fukushima M (2006b) Anthocyanin-rich purple potato flake extract has antioxidant capacity and improves antioxidant potential in rats. *Br J Nutr* 96(6):1125–1133
- Han KH, Matsumoto A, Shimada K, Sekikawa M, Fukushima M (2007a) Effects of anthocyanin-rich purple potato flakes on antioxidant status in F344 rats fed a cholesterol-rich diet. *Br J Nutr* 98(5):914–921
- Han KH, Shimada K, Sekikawa M, Fukushima M (2007b) Anthocyanin-rich red potato flakes affect serum lipid peroxidation and hepatic SOD mRNA level in rats. *Biosci Biotechnol Biochem* 71(5):1356–1359
- Hansen AA (1925) Two fatal cases of potato poisoning. *Science* 61(1578):340–341
- Harris PM (ed) (1978) The potato crop: the scientific basis for improvement. Chapman & Hall, London, 730 pp
- Hasegawa S, Johnson RM, Gould WA (1966) Effect of cold storage on chlorogenic acid content of potatoes. *J Agric Food Chem* 14(2):165–169
- Hashimoto N, Nakamura Y, Noda T, Han KH, Fukushima M (2011) Effects of feeding potato pulp on cholesterol metabolism and its association with cecal conditions in rats. *Plant Foods Hum Nutr* 66(4):401–407
- Hayward A, Stirnberg P, Beveridge C, Leyser O (2009) Interactions between auxin and strigolactone in shoot branching control. *Plant Physiol* 151(1):400–412
- Hellenäs K-E, Nyman A, Slanina P, Löf L, Gabrielsson J (1992) Determination of potato glycoalkaloids and their aglycone in blood serum by high-performance liquid chromatography. Application to pharmacokinetic studies in humans. *J Chromatogr* 573(1):69–78
- Hellenäs K-E, Branzell C, Johnsson H, Slanina P (1995a) Glycoalkaloid content of early potato varieties. *J Sci Food Agric* 67(1):125–128
- Hellenäs K-E, Branzell C, Johnsson H, Slanina P (1995b) High levels of glycoalkaloids in the established Swedish potato variety Magnum Bonum. *J Sci Food Agric* 68(2):249–255
- Ho CT, Coleman EC (1980) Chemistry of baked potato flour: further identification of heterocyclic compounds in the volatile flavor of baked potato. *J Food Sci* 45(4):1094–1095
- Ho CT, Coleman EC (1981) Halogen compounds identified in the volatile constituents of baked potatoes. *J Agric Food Chem* 29(1):200–201
- Hossain MB, Tiwari BK, Gangopadhyay N, O'Donnell CP, Brunton NP, Rai DK (2014) Ultrasonic extraction of steroidal alkaloids from potato peel waste. *Ultrason Sonochem* 21(4):1470–1476
- Huxtable RJ (1992) The toxicology of alkaloids in foods and herbs. In: Tu AT (ed) Handbook of natural toxins, vol 7, Food poisoning. Marcel Dekker, Inc., New York, pp 237–263

- Hylla S, Gostner A, Dusel G, Anger H, Bartram HP, Christl SU, Kasper H, Scheppach W (1998) Effects of resistant starch on the colon in healthy volunteers: possible implications for cancer prevention. *Am J Clin Nutr* 67:136–142
- Iablokov V, Sydora BC, Foshaug R, Meddings J, Driedger D, Churchill T, Fedorak RN (2010) Naturally occurring glycoalkaloids in potatoes aggravate intestinal inflammation in two mouse models of inflammatory bowel disease. *Dig Dis Sci* 55(11):3078–3085
- Im HW, Suh BS, Lee SU, Kozukue N, Ohnisi-Kameyama M, Levin CE, Friedman M (2008) Analysis of phenolic compounds by high-performance liquid chromatography and liquid chromatography/mass spectrometry in potato plant flowers, leaves, stems, and tubers and in home-processed potatoes. *J Agric Food Chem* 56(9):3341–3349
- Jansen G, Flamme W (2006) Coloured potatoes (*Solanum tuberosum* L.) – anthocyanin content and tuber quality. *Genet Resour Crop Evol* 53(7):1321–1331
- Järvinen R, Silvestre AJ, Holopainen U, Kaimainen M, Nyssölä A, Gil AM, Pascoal Neto C, Lehtinen P, Buchert J, Kallio H (2009) Suberin of potato (*Solanum tuberosum* var. Nikola): comparison of the effect of cutinase CcCut1 with chemical depolymerization. *J Agric Food Chem* 57(19):9016–9027
- Jobling SA, Schwall GP, Westcott RJ, Sidebottom CM, Debet M, Gidley MJ, Jeffcoat R, Safford R (1999) A minor form of starch branching enzyme in potato (*Solanum tuberosum* L.) tubers has a major effect on starch structure: cloning and characterisation of multiple forms of SBE A. *Plant J* 18(2):163–171
- Jocković N, Fischer W, Brandsch M, Brandt W, Dräger B (2013) Inhibition of human intestinal α -glucosidases by calystegines. *J Agric Food Chem* 61(23):5550–5557
- Johnson DF, Bennet RD, Heftmann E (1963) Cholesterol in higher plants. *Science* 140:198–199
- Johnson DF, Heftmann E, Houghland GVC (1964) The biosynthesis of sterols in *Solanum tuberosum*. *Arch Biochem Biophys* 104(1):102–105
- Joint FAO/WHO Expert Committee on Food Additives (JECFA) (1993) Solanine and chacocine. In: Toxicologic evaluation of certain food additives and naturally occurring toxicants, prepared by the 39th meeting of JECFA, WHO food additives series 30. World Health Organization, Geneva, Switzerland
- Jones PG, Fenwick GR (1981) The glycoalkaloid content of some edible solanaceous fruits and potato products. *J Sci Food Agric* 32(4):419–421
- Josephson DB, Lindsay RC (1987) c4-Heptenal: an influential volatile compound in boiled potato flavor. *J Food Sci* 52(2):328–331
- Kapoor AC, Desborough SL, Li PH (1975) Potato tuber proteins and their nutritional quality. *Potato Res* 18(3):469–478
- Karlsson ME, Eliasson AC (2003) Effects of time/temperature treatments on potato (*Solanum tuberosum*) starch: a comparison of isolated starch and starch in situ. *J Sci Food Agric* 83(15):1587–1592
- Karlsson MF, Birgersson G, Cotes Prado AM, Bosa F, Bengtsson M, Witzgall P (2009) Plant odor analysis of potato: response of guatemalan moth to above- and below ground potato volatiles. *J Agric Food Chem* 57(13):5903–5909
- Karlsson MF, Birgersson G, Witzgall P, Lekkfeldt JD, Nimal Punyasiri PA, Bengtsson M (2013) Guatemalan potato moth *Tecia solanivora* distinguish odour profiles from qualitatively different potatoes *Solanum tuberosum* L. *Phytochemistry* 85:72–81
- Kaspar KL, Park JS, Brown CR, Mathison BD, Navarre DA, Chew BP (2011) Pigmented potato consumption alters oxidative stress and inflammatory damage in men. *J Nutr* 141(1):108–111
- Kaspar KL, Park JS, Brown CR, Weller K, Ross CF, Mathison BD, Chew BP (2013) Sensory evaluation of pigmented flesh potatoes (*Solanum tuberosum* L.). *Food Nutr Sci* 4(1):Article ID 26766
- Kaur L, Singh N, Sodhi NS (2002) Some properties of potatoes and their starches II. Morphological, thermal and rheological properties of starches. *Food Chem* 79(2):183–192
- Kaur A, Singh N, Ezekiel R, Guraya HS (2007) Physicochemical, thermal and pasting properties of starches separated from different potato cultivars grown at different locations. *Food Chem* 101(2):643–651
- Kayonga A, Habiaremye FX (1987) Médecine traditionnelle et plantes médicinales rwandaises. Contribution aux études ethnobotaniques de la flore rwandaise. Préfecture de Gisenyi. Univ. Nat. Rwanda Centre universitaire de recherche sur la pharmacopée et la médecine traditionnelle, CURPHAMETRA, inédit, 121 pp (in French)
- Keeler RF, Baker DC, Gaffield W (1990) Spirosolane-containing *Solanum* species and induction of congenital craniofacial malformations. *Toxicol* 28(8):873–884
- Kenny OM, McCarthy CM, Brunton NP, Hossain MB, Rai DK, Collins SG, Jones PW, Maguire AR, O'Brien NM (2013) Anti-inflammatory properties of potato glycoalkaloids in stimulated Jurkat and Raw 264.7 mouse macrophages. *Life Sci* 92(13):775–782
- Keswani MH, Vartak AM, Patil A, Davies JW (1990) Histological and bacteriological studies of burn wounds treated with boiled potato peel dressings. *Burns* 16(2):137–143
- Keukens EA, de Vrije T, Fabrie CH, Demel RA, Jongen WM, de Kruijff B (1992) Dual specificity of sterol-mediated glycoalkaloid induced membrane disruption. *Biochim Biophys Acta* 1110(2):127–136
- Keukens EA, de Vrije T, van den Boom C, de Waard P, Plasman HH, Thiel F, Chupin V, Jongen WM, de Kruijff B (1995) Molecular basis of glycoalkaloid induced membrane disruption. *Biochim Biophys Acta* 1240(2):216–228
- Keukens EA, de Vrije T, Jansen LA, de Boer H, Janssen M, de Kroon AI, Jongen WM, de Kruijff B (1996) Glycoalkaloids selectively permeabilize cholesterol containing biomembranes. *Biochim Biophys Acta* 1279(2):243–250

- Khalilova AZ, Paramonov EA, Baltaev UA, Odinkov VN, Khalilov LM (1997) Cyclic sesquiterpenes in the volatile secretions of potato leaves (*Solanum tuberosum* L.) and Colorado beetle (*Leptinotarsa decemlineata* Say). Russ Chem Bull 46(10):1805
- Khan I, Muller K, Warmbier H (1977) Einfluss von sorte und düngung auf das spektrum flüchtiger aromastoffe in kartoffeln. (Effects of variety and fertilizer on the volatile aromatic spectrum of potatoes). Potato Res 20:235–242
- Kim SY, Wiesenborn DP, Orr PH, Grant LA (1995) Screening potato starch for novel properties using differential scanning calorimetry. J Food Sci 60:1060–1065
- King RR (1980) Analysis of potato glycoalkaloids by gas–liquid chromatography of alkaloid components. J Assoc Off Anal Chem 63(6):1226–1230
- Kita A, Bąkowska-Barczak A, Hamouz K, Kułakowska K, Lisińska G (2013) The effect of frying on anthocyanin stability and antioxidant activity of crisps from red- and purple-fleshed potatoes (*Solanum tuberosum* L.). J Food Comp Anal 32(2):169–175
- Kita A, Bąkowska-Barczak A, Lisińska G, Hamouz K, Kułakowska K (2014) Antioxidant activity and quality of red and purple flesh potato chips. LWT-Food Sci Technol 62(1) Part 2:525–531
- Knowles LO, Knowles NR (2012) Toxicity and metabolism of exogenous α , β -unsaturated carbonyls in potato (*Solanum tuberosum* L.) tubers. J Agric Food Chem 60(44):11173–11181
- Koda Y (1982) Changes in levels of butanol- and water-soluble cytokinins during the life cycle of potato tubers. Plant Cell Physiol 23(5):843–849
- Koda Y, Okazawa Y (1988) Detection of potato tuber-inducing activity in potato leaves and old tubers. Plant Cell Physiol 29:969–974
- Koda Y, Omer EA, Yoshihara T, Shibata H, Sakamura S, Okazawa Y (1988) Isolation of a specific potato tuber-inducing substance from potato leaves. Plant Cell Physiol 29:1047–1051
- Koda Y, Kikuta Y, Tazaki H, Tsujino Y, Sakamura S, Yoshihara T (1991) Potato tuber-inducing activities of jasmonic acid and related compounds. Phytochemistry 30:1435–1438
- Koda Y, Kikuta Y, Kitahara T, Nishi T, Mori K (1992a) Comparisons of various biological activities of stereoisomers of methyl jasmonate. Phytochemistry 31:1111–1114
- Koda Y, Takahashi K, Kikuta Y (1992b) Potato tuber-inducing activities of salicylic acid and related compounds. J Plant Growth Reg 11(4):215–219
- Koehler PE, Mason ME, Odell GV (1971) Odor threshold levels of pyrazine compounds and assessment of their role in the flavor of roasted foods. J Food Sci 36(5):816–818
- Kon SK (1928) The nutritional value of tuberin, the globulin of potato. Biochem J 22(1):261–267
- Kong AH, Fuenzalida C, Hess S, Contreras A, Vega-Gálvez A, Lemus-Mondaca R (2012) Capacidad antioxidante y compuestos fenólicos totales de una selección de doce variedades tradicionales de papa cultivadas en la región sur de Chile. Chilean J Agric Res 72(1):3–9
- Kozukue N, Kozukue E, Mizuno S (1987) Glycoalkaloids in potato plants and tubers. HortScience 22:294–296
- Kozukue N, Misoo S, Yamada T, Kamijima O, Friedman M (1999) Inheritance of morphological characters and glycoalkaloids in potatoes of somatic hybrids between dihaploid *Solanum acaule* and tetraploid *Solanum tuberosum*. J Agric Food Chem 47(10):4478–4483
- Kröner A, Marnet N, Andrivon D, Val F (2012) Nicotiflorin, rutin and chlorogenic acid: phenylpropanoids involved differently in quantitative resistance of potato tubers to biotrophic and necrotrophic pathogens. Plant Physiol Biochem 57:23–31
- Kubow S, Hobson L, Iskandar MM, Sabally K, Donnelly DJ, Agellon LB (2014) Extract of Irish potatoes (*Solanum tuberosum* L.) decreases body weight gain and adiposity and improves glucose control in the mouse model of diet-induced obesity. Mol Nutr Food Res 58:2235–2238
- Kuc J (1984) Steroid glycoalkaloids and related compounds as potato quality factors. Am Potato J 61(3):123–139
- Kvasnicka F, Jockovic N, Dräger B, Sevcík R, Cepl J, Voldrich M (2008) Electrophoretic determination of calystegines A3 and B2 in potato. J Chromatogr A 1181(1–2):137–144
- Lachman J, Hamouz K (2005) Red and purple coloured potatoes as a significant antioxidant source in human nutrition- a review. Plant Soil Environ 51(11):477–482
- Lachman J, Hamouz K, Sulc M, Orsák M, Dvorak P (2008) Differences in phenolic content and antioxidant activity in yellow and purple-fleshed potatoes grown in the Czech Republic. Plant Soil Environ 54(1):1–6
- Lachman J, Hamouz K, Orsák M, Pivec V, Hejtmánková K, Pazderů K, Dvořák P, Čepl J (2012) Impact of selected factors—cultivar, storage, cooking and baking on the content of anthocyanins in coloured-flesh potatoes. Food Chem 133(4):1107–1116
- Lachman J, Hamouz K, Musilová J, Hejtmánková K, Kotíková Z, Pazderů K, Domkářová J, Pivec V, Cimr J (2014) Effect of peeling and three cooking methods on the content of selected phytochemicals in potato tubers with various colour of flesh. Food Chem 161:224–229
- Lampitt LH, Bushill JH, Rooke HS, Jackson EM (1943) Solanine, glycoside of the potato. II. Its distribution in the potato plant. J Soc Chem Ind 62(4):48–51
- Langkilde S, Schröder M, Stewart D, Meyer O, Conner S, Davies H, Poulsen M (2008) Acute toxicity of high doses of the glycoalkaloids, alpha-solanine and alpha-chaconine, in the Syrian Golden hamster. J Agric Food Chem 56(18):8753–8760
- Langkilde S, Mandimika T, Schröder M, Meyer O, Slob W, Peijnenburg A, Poulsen M (2009) A 28-day repeat dose toxicity study of steroidal glycoalkaloids, alpha-solanine and alpha-chaconine in the Syrian Golden hamster. Food Chem Toxicol 47(6):1099–1108

- Langkilde S, Schröder M, Frank T, Shepherd LV, Conner S, Davies HV, Meyer O, Danier J, Rychlik M, Belknap WR, McCue KF, Engel KH, Stewart D, Knudsen I, Poulsen M (2012) Compositional and toxicological analysis of a GM potato line with reduced α -solanine content – a 90-day feeding study in the Syrian Golden hamster. *Regul Toxicol Pharmacol* 64(1):177–185
- Langner E, Nunes FM, Pozarowski P, Kandefer-Szerszeń M, Pierzynowski SG, Rzeski W (2011) Antiproliferative activity of melanoidins isolated from heated potato fiber (Potex) in glioma cell culture model. *J Agric Food Chem* 59(6):2708–2716
- Langner E, Nunes FM, Pożarowski P, Kandefer-Szerszeń M, Pierzynowski SG, Rzeski W (2013) Melanoidins isolated from heated potato fiber (Potex) affect human colon cancer cells growth via modulation of cell cycle and proliferation regulatory proteins. *Food Chem Toxicol* 57:246–255
- Lee JH, Pangloli P (2013) Volatile compounds and storage stability of potato chips fried in mid-oleic sunflower oil. *Int J Food Prop* 16(3):563–573
- Lee KR, Kozukue N, Han JS, Park JH, Chang EY, Baek EJ, Chang JS, Friedman M (2004) Glycoalkaloids and metabolites inhibit the growth of human colon (HT29) and liver (HepG2) cancer cells. *J Agric Food Chem* 52:2832–2839
- Lee SJ, Shin JS, Choi HE, Lee KG, Cho YW, An HJ, Jang DS, Jeong JC, Kwon OK, Nam JH, Lee KT (2014) Chloroform fraction of *Solanum tuberosum* L. cv Jayoung epidermis suppresses LPS-induced inflammatory responses in macrophages and DSS-induced colitis in mice. *Food Chem Toxicol* 63:53–61
- Leeman M, Ostman E, Björck I (2005) Vinegar dressing and cold storage of potatoes lowers postprandial glycaemic and insulinaemic responses in healthy subjects. *Eur J Clin Nutr* 59(11):1266–1271
- Leeman M, Ostman E, Björck I (2008) Glycaemic and satiating properties of potato products. *Eur J Clin Nutr* 62(1):87–95
- Leo L, Leone A, Longo C, Lombardi DA, Raimo F, Zacheo G (2008) Antioxidant compounds and antioxidant activity in “early potatoes”. *J Agric Food Chem* 56(11):4154–4163
- Lewis CE, Walker JRL, Lancaster JE, Sutton KH (1998a) Determination of anthocyanins, flavonoids and phenolic acids in potatoes. I: coloured cultivars of *Solanum tuberosum* L. *J Sci Food Agric* 77:45–57
- Lewis CE, Walker JRL, Lancaster JE, Sutton KH (1998b) Determination of anthocyanins, flavonoids and phenolic acids in potatoes. II: wild, tuberous *Solanum* species. *J Sci Food Agric* 77:58–63
- Lewis CE, Walker JRL, Lancaster JE (1999) Changes in anthocyanin, flavonoid and phenolic acid concentrations during development and storage of coloured potato (*Solanum tuberosum* L.) tubers. *J Sci Food Agric* 79:311–316
- Liang SB, McDonald AG (2014) Chemical and thermal characterization of potato peel waste and its fermentation residue as potential resources for biofuel and bio-products production. *J Agric Food Chem* 62(33):8421–8429
- Lindhauer MG, De Fekete MAR (1990) Starch synthesis in potato (*Solanum tuberosum*) tubers: activity of selected enzymes in dependence of potassium content in storage tissue. In: Van Beusichem ML (ed) *Plant nutrition—physiology and applications*. Springer, Netherlands, pp 643–647
- Lindner J, Jaschik S, Korpacz J (1960) Amino acid composition and biological value of potato protein fractions. *Qual Plant Mater Veg* 7:290–294
- Lisinska G, Leszczynski W (1989) Potato tubers as a raw material for processing and nutrition. In: Lisinska G, Leszczynski W (eds) *Potato science and technology*. Elsevier Applied Science, London
- Liu YW, Han CH, Lee MH, Hsu FL, Hou WC (2003) Patatin, the tuber storage protein of potato (*Solanum tuberosum* L.), exhibits antioxidant activity in vitro. *J Agric Food Chem* 51(15):4389–4393
- Lojzova L, Riddellova K, Hajslova J, Zrostlikova J, Schurek J, Cajka T (2009) Alternative GC–MS approaches in the analysis of substituted pyrazines and other volatile aromatic compounds formed during Maillard reaction in potato chips. *Anal Chim Acta* 641(1–2):101–109
- Lui LH, Vikram A, Abu-Nada Y, Kushalappa AC, Raghavan GSV, Al-Mughrabi K (2005) Volatile metabolic profiling for discrimination of potato tubers inoculated with dry and soft rot pathogens. *Am J Potato Res* 82(1):1–8
- Mäder J, Rawel H, Kroh LW (2009) Composition of phenolic compounds and glycoalkaloids alpha-solanine and alpha-chaconine during commercial potato processing. *J Agric Food Chem* 57(14):6292–6297
- Madiwale GP, Reddivari L, Holm DG, Vanamala J (2011) Storage elevates phenolic content and antioxidant activity but suppresses antiproliferative and pro-apoptotic properties of colored-flesh potatoes against human colon cancer cell lines. *J Agric Food Chem* 59(15):8155–8166
- Madiwale GP, Reddivari L, Stone M, Holm DG, Vanamala J (2012) Combined effects of storage and processing on the bioactive compounds and pro-apoptotic properties of color-fleshed potatoes in human colon cancer cells. *J Agric Food Chem* 60(44):11088–11096
- Maga JA (1994) Potato flavor. *Food Rev Int* 10(1):1–48
- Mandimika T, Baykus H, Poortman J, Garza C, Kuiper H, Peijnenburg A (2008) PI3K/AKT, JNK, and ERK pathways are not crucial for the induction of cholesterol biosynthesis gene transcription in intestinal epithelial cells following treatment with the potato glycoalkaloid alpha-chaconine. *J Agric Food Chem* 56(18):8745–8752
- Martin FL, Ames JM (2001) Comparison of flavor compounds of potato chips fried in palmolein and silicone fluid. *J Am Oil Chem Soc* 78(8):863–866
- Matsuura-Endo C, Ohara-Takada A, Chuda Y, Ono H, Yada H, Yoshida M, Kobayashi A, Tsuda S, Takigawa S, Noda T, Yamauchi H, Mori M (2006) Effects of

- storage temperature on the contents of sugars and free amino acids in tubers from different potato cultivars and acrylamide in chips. *Biosci Biotechnol Biochem* 70(5):1173–1180
- Mattila P, Hellström J (2007) Phenolic acids in potatoes, vegetables, and some of their products. *J Food Comp Anal* 20:152–160
- Mattinen ML, Filpponen I, Järvinen R, Li B, Kallio H, Lehtinen P, Argyropoulos D (2009) Structure of the polyphenolic component of suberin isolated from potato (*Solanum tuberosum* var. Nikola). *J Agric Food Chem* 57(20):9747–9753
- Mazza G, Pietrzak EM (1990) Headspace volatiles and sensory characteristics of earthy, musty flavoured potatoes. *Food Chem* 36:97–112
- McGill CR, Kurilich AC, Davignon J (2013) The role of potatoes and potato components in cardiometabolic health: a review. *Ann Med* 45(7):467–473
- McMillan M, Thompson JC (1979) An outbreak of suspected solanine poisoning in schoolboys: examinations of criteria of solanine poisoning. *Q J Med* 48(190):227–243
- Meigh DF, Filmer AAE, Self R (1973) Growth-inhibitory volatile aromatic compounds produced by *Solanum tuberosum* tubers. *Phytochemistry* 12:987–993
- Mensinga TT, Sips AJ, Rempelberg CJ, van Twillert K, Meulenbelt J, van den Top HJ, van Egmond HP (2005) Potato glycoalkaloids and adverse effects in humans: an ascending dose study. *Regul Toxicol Pharmacol* 41(1):66–72
- Miao YT, Zhang HJ, Zhang LL, Wu SJ, Sun YJ, Shan Y, Yuan Y (2014) Acrylamide and 5-hydroxymethylfurfural formation in reconstituted potato chips during frying. *J Food Sci Technol* 51(12):4005–4011
- Miča B (1976) Charakteristik der stärke ausgewählter kartoffelsorten teil 2. Gehalt an phosphor, kalium und calcium in der stärke. *Starch/Stärke* 28:410–413
- Miranda L, Deußer H, Evers D (2013) The impact of in vitro digestion on bioaccessibility of polyphenols from potatoes and sweet potatoes and their influence on iron absorption by human intestinal cells. *Food Funct* 4(11):1595–1601
- Mohdaly AAA, Sarhan MA, Smetanska I, Mahmoud A (2010) Antioxidant properties of various solvent extracts of potato peel, sugar beet pulp and sesame cake. *J Sci Food Agric* 90(2):218–226
- Mohdaly AAA, Hassanien MFR, Mahmoud A, Sarhan MA, Smetanska I (2013) Phenolic extracted from potato, sugar beet, and sesame processing by-products. *Int J Food Prop* 16(5):1148–1168
- Mondy NI, Gosselin B (1988) Effect of peeling on total phenols, total glycoalkaloids, discoloration and flavor of cooked potatoes. *J Food Sci* 53(3):756–759
- Mookherjee BD, Deck RE, Chang SS (1965) Food flavor changes, relationship between monocarbonyl compounds and flavor of potato chips. *J Agric Food Chem* 13(2):131–134
- Morris SC, Lee TH (1984) The toxicity and teratogenicity of solanaceae glycoalkaloids, particularly those of the potato (*Solanum tuberosum*): a review. *Food Technol Aus* 36:118–124
- Morris WL, Ross HA, Ducreux LJ, Bradshaw JE, Bryan GJ, Taylor MA (2007) Umami compounds are a determinant of the flavor of potato (*Solanum tuberosum* L.). *J Agric Food Chem* 55(23):9627–9633
- Morris WL, Shepherd T, Verrall SR, McNicol JW, Taylor MA (2010) Relationships between volatile and non-volatile metabolites and attributes of processed potato flavour. *Phytochemistry* 71(14–15):1765–1773
- Morris WL, Ducreux LJ, Shepherd T, Lewinsohn E, Davidovich-Rikanati R, Sitrit Y, Taylor MA (2011) Utilisation of the MVA pathway to produce elevated levels of the sesquiterpene α -copaene in potato tubers. *Phytochemistry* 72(18):2288–2293
- Mosley AR, Chase RW (1993) Selecting cultivars and obtaining healthy seed lots. In: Rowe RC (ed) *Potato health management*. APS Press, St Paul, pp 193
- Mottram DS, Wedzicha BL, Dodson AT (2002) Acrylamide is formed in the Maillard reaction. *Nature* 419(6906):448–449
- Mulinacci N, Ieri F, Giaccherini C, Innocenti M, Andrenelli L, Canova G, Saracchi M, Casiraghi MC (2008) Effect of cooking on the anthocyanins, phenolic acids, glycoalkaloids, and resistant starch content in two pigmented cultivars of *Solanum tuberosum* L. *J Agric Food Chem* 56(24):11830–11837
- Mullin WJ, Wolynetz MS, Emery JP, Brooks L (1993) The effect of variety, growing location, and storage on the dietary fiber content of potatoes. *J Food Comp Anal* 6(4):316–323
- Mutti B, Grosch W (1999) Potent odorants of boiled potatoes. *Nahrung* 43:302–306
- Muttucumaru N, Elmore JS, Curtis T, Mottram DS, Parry MA, Halford NG (2008) Reducing acrylamide precursors in raw materials derived from wheat and potato. *J Agric Food Chem* 56(15):6167–6172
- Muttucumaru N, Keys AJ, Parry MA, Powers SJ, Halford NG (2014a) Photosynthetic assimilation of ^{14}C into amino acids in potato (*Solanum tuberosum*) and asparagine in the tubers. *Planta* 239(1):161–170
- Muttucumaru N, Powers SJ, Elmore JS, Briddon A, Mottram DS, Halford NG (2014b) Evidence for the complex relationship between free amino acid and sugar concentrations and acrylamide-forming potential in potato. *Ann Appl Biol* 164(2):286–300
- Naito K, Umemura Y, Mori M, Sumida T, Okada T, Takamatsu N, Okawa Y, Hayashi K, Saito N, Honda T (1998) Acylated pelargonidin glycosides from a red potato. *Phytochemistry* 47(1):109–112
- Nakamura T, Komori C, Lee Y, Hashimoto F, Yahara S, Nohara T, Ejima J (1996) Cytotoxic activities of *Solanum* steroidal glycosides. *Biol Pharm Bull* 19(4):564–566
- Nakasone K, Hayashi R, Hata T (1972) Composition of potato proteins. *Nippon Nogei Kagakukai J* 46:45–50

- Nara K, Miyoshi T, Honma T, Koga H (2006) Antioxidative activity of bound-form phenolics in potato peel. *Biosci Biotechnol Biochem* 70(6):1489–1491
- Narváez-Cuenca CE, Vincken JP, Zheng C, Gruppen H (2013) Diversity of (dihydro) hydroxycinnamic acid conjugates in Colombian potato tubers. *Food Chem* 139(1–4):1087–1097
- Nash RJ, Rothschild M, Porter EA, Watsion AA, Waigh RD, Waterman PG (1993) Calystegines in *Solanum* and *Datura* species and the death's-head hawk-moth (*Acherontia atropus*). *Phytochemistry* 34:1281–1283
- Navarre DA, Pillai SS, Shakya R, Holden MJ (2011) HPLC profiling of phenolics in diverse potato genotypes. *Food Chem* 127:34–41
- Navarre DA, Payyavula RS, Shakya R, Knowles NR, Pillai SS (2013) Changes in potato phenylpropanoid metabolism during tuber development. *Plant Physiol Biochem* 65:89–101
- Nikolic NC, Stankovic MZ (2003) Solanidine hydrolytic extraction and separation from the potato (*Solanum tuberosum* L.) vines by using solid–liquid–liquid systems. *J Agric Food Chem* 51(7):1845–1849
- Nisha P, Singhal RS, Pandit AB (2009) A study on degradation kinetics of niacin in potato (*Solanum tuberosum* L.). *J Food Comp Anal* 22(6):620–624
- Nnomo RD, Tchouamo IR, Pinta JY (2009) Apiphythérapie à base du miel au Cameroun. *Ethnopharmacologia* 44:56–63 (in French)
- Noda T, Kottearachchi NS, Tsuda S, Mori M, Takigawa S, Matsuura-Endo C, Kim SJ, Hashimoto N, Yamauchi H (2007) Starch phosphorus content in potato (*Solanum tuberosum* L.) cultivars and its effect on other starch properties. *Carbohydr Polym* 68(4):793–796
- Nowacki W (2009) Characteristics of native potato cultivars register. *Plant Breeding and Acclimatization Institute, Jadwisin*, pp 1–34 (in Polish)
- Nursten HE, Sheen MR (1974) Volatile flavour components of cooked potato. *J Sci Food Agric* 25(6):643–663
- Nwokocha LM, Aviria NA, Senan C, Williams PA (2014) A comparative study of properties of starches from Irish potato (*Solanum tuberosum*) and sweet potato (*Ipomea batatas*) grown in Nigeria. *Starch-Stärke* 66(7–8):714–723
- Ohara-Takada A, Matsuura-Endo C, Chuda Y, Ono H, Yada H, Yoshida M, Kobayashi A, Tsuda S, Takigawa S, Noda T, Yamauchi H, Mori M (2005) Change in content of sugars and free amino acids in potato tubers under short-term storage at low temperature and the effect on acrylamide level after frying. *Biosci Biotechnol Biochem* 69(7):1232–1238
- Okeke BC, Frankenberger WT Jr (2005) Use of starch and potato peel waste for perchlorate bioreduction in water. *Sci Total Environ* 347(1–3):35–45
- Onyeneho SN, Hettiarachchy NS (1993) Antioxidant activity, fatty acids and phenolic acids compositions of potato peels. *J Sci Food Agric* 62(4):345–350
- Oruna-Concha MJ, Duckham SC, Ames JM (2001) Comparison of volatile compounds isolated from the skin and flesh of four potato cultivars after baking. *J Agric Food Chem* 49(5):2414–2421
- Oruna-Concha MJ, Bakker J, Ames JM (2002a) Comparison of the volatile components of eight cultivars of eight cultivars of potato after microwave baking. *LWT food Sci Technol* 35(1):80–86
- Oruna-Concha MJ, Bakker J, Ames JM (2002b) Comparison of the volatile components of two cultivars of potato cooked by boiling, conventional baking and microwave baking. *J Sci Food Agric* 82(9):1080–1087
- Osborne TC, Campbell GF (1896) The proteides of potato. *J Am Chem Soc* 18:575–582
- Osske G, Schreiber K (1965) 24-methylen-lophenol, ein neues 4 α -methyl-sterin aus *Saccharum officinarum* L. und *Solanum tuberosum* L. sterine und triterpenoide. VI. Mitteilung. *Tetrahedron* 21:1559–1566
- Ostrý V, Ruprich J, Skarkova J (2010) Glycoalkaloids in potato tubers: the effect of peeling and cooking in salted water. *Acta Aliment* 39(2):130–135
- Paiva E, Lister RM, Park WD (1983) Induction and accumulation of major tuber proteins of potato stems and petioles. *Plant Physiol* 71:161–168
- Parada J, Aguilera JM (2009) In vitro digestibility and glycemic response of potato starch is related to granule size and degree of gelatinization. *J Food Sci* 74(1):E34–E38
- Pareles SR, Chang SS (1974) Identification of compounds responsible for baked potato flavor. *J Agric Food Chem* 22(2):339–340
- Park WD, Blackwood C, Mignery GA, Hermodson MA, Lister RM (1983) Analysis of the heterogeneity of the 40,000 molecular weight tuber glycoprotein of potatoes by immunological methods and by NH₂-terminal sequence analysis. *Plant Physiol* 71:156–160
- Parr AJ, Mellon FA, Colquhoun IJ, Davies HV (2005) Dihydrocaffeoyl polyamines (kukoamine and allies) in potato (*Solanum tuberosum*) tubers detected during metabolite profiling. *J Agric Food Chem* 53(13):5461–5466
- Pasare SA, Ducreux LJ, Morris WL, Campbell R, Sharma SK, Roumeliotis E, Kohlen W, van der Krol S, Bramley PM, Roberts AG, Fraser PD, Taylor MA (2013) The role of the potato (*Solanum tuberosum*) CCD8 gene in stolon and tuber development. *New Phytol* 198(4):1108–1120
- Patel B, Schutte R, Sporns P, Doyle J, Jewel L, Fedorak RN (2002) Potato glycoalkaloids adversely affect intestinal permeability and aggravate inflammatory bowel disease. *Inflamm Bowel Dis* 8(5):340–346
- Payyavula RS, Navarre DA, Kuhl JC, Pantoja A, Pillai SS (2012) Differential effects of environment on potato phenylpropanoid and carotenoid expression. *BMC Plant Biol* 12:39
- Payyavula RS, Navarre DA, Kuhl J, Pantoja A (2013) Developmental effects on phenolic, flavonol, anthocyanin, and carotenoid metabolites and gene expression in potatoes. *J Agric Food Chem* 61(30):7357–7365
- Pęksa A, Golubowska G, Rytel E, Lisinska G, Aniolowski K (2002) Influence of harvest date on glycoalkaloid

- contents of three potato varieties. *Food Chem* 78(3):313–317
- Pęksa A, Gołubowska G, Aniołowski K, Lisińska G, Rytel E (2006) Changes of glycoalkaloids and nitrate contents in potatoes during chip processing. *Food Chem* 97(1):151–156
- Pęksa A, Kita A, Kułakowska K, Aniołowska M, Hamouz K, Nemś A (2013) The quality of protein of coloured fleshed potatoes. *Food Chem* 141(3):2960–2966
- Percival G, Dixon GR, Sword A (1996) Glycoalkaloid concentration of potato tubers following exposure to daylight. *J Sci Food Agric* 71(1):59–63
- Petersen MA, Poll L, Larsen LM (1998) Comparison of volatiles in raw and boiled potatoes using a mild extraction technique combined with GC odour profiling and GC–MS. *Food Chem* 61(4):461–466
- Petersen MA, Poll L, Larsen LM (1999) Identification of compounds contributing to boiled potato off-flavour ('POF'). *LWT-Food Sci Technol* 32(1):32–40
- Pettersson EV, Arif U, Schulzova V, Krtková V, Hajšlová J, Meijer J, Andersson HC, Jonsson L, Sitbon F (2013) Glycoalkaloid and calystegine levels in table potato cultivars subjected to wounding, light, and heat treatments. *J Agric Food Chem* 61(24):5893–5902
- Phillips BJ, Hughes JA, Phillips JC, Walters DG, Anderson D, Tahourdin CS (1996) A study of the toxic hazard that might be associated with the consumption of green potato tops. *Food Chem Toxicol* 34(5):439–448
- Pihlanto A, Akkanen S, Korhonen HJ (2008) ACE-inhibitory and antioxidant properties of potato (*Solanum tuberosum*). *Food Chem* 109(1):104–112
- Piletska EV, Burns R, Terry LA, Piletsky SA (2012) Application of a molecularly imprinted polymer for the extraction of kukoamine A from potato peels. *J Agric Food Chem* 60(1):95–99
- Ponasik JA, Strickland C, Faerman C, Savvides S, Karplus PA, Ganem B (1995) Kukoamine A and other hydrophobic acylpolyamines: potent and selective inhibitors of *Crithidia fasciculata* trypanothione reductase. *Biochem J* 311:371–375
- Pots AM, de Jongh HH, Gruppen H, Hamer RJ, Voragen AG (1998) Heat-induced conformational changes of patatin, the major potato tuber protein. *Eur J Biochem* 252(1):66–72
- Powers SJ, Mottram DS, Curtis A, Halford NG (2013) Acrylamide concentrations in potato crisps in Europe from 2002 to 2011. *Food Addit Contam Part A Chem Anal Control Expo Risk Assess* 30(9):1493–1500
- Purseglove JW (1968) Tropical crops: Dicotyledons. 1 & 2. Longman, London, 719 pp
- Raben A, Tagliabue A, Christensen NJ, Madsen J, Host JJ, Astrup A (1994) Resistant starch: the effect on post-prandial glycemia, hormonal response, and satiety. *Am J Clin Nutr* 60:544–551
- Raben A, Andersen K, Karberg MA, Holst JJ, Astrup A (1997) Acetylation of or beta-cyclodextrin addition to potato beneficial effect on glucose metabolism and appetite sensations. *Am J Clin Nutr* 66(2):304–314
- Racusen D, Foote M (1980) A major soluble glycoprotein of potato tubers. *J Food Biochem* 4:43–52
- Ramdath DD, Padhi E, Hawke A, Sivaramalingam T, Tsao R (2014) The glycemic index of pigmented potatoes is related to their polyphenol content. *Food Funct* 5(5):909–915
- Raponda-Walker A, Sillans R (1995) Les Plantes Utiles du Gabon. Encyclopédie Biologique. Editions Sepia, 697 pp (First Published 1961)
- Reddivari L, Hale AL, Miller JC (2007a) Determination of phenolic content, composition and their contribution to antioxidant activity in specialty potato selections. *Am J Potato Res* 84(4):275–282
- Reddivari L, Hale AL, Miller JC Jr (2007b) Genotype, location, and year influence antioxidant activity, carotenoid content, phenolic content, and composition in specialty potatoes. *J Agric Food Chem* 55(20):8073–8079
- Reddivari L, Vanamala J, Chintharlapalli S, Safe SH, Miller JC Jr (2007c) Anthocyanin fraction from potato extracts is cytotoxic to prostate cancer cells through activation of caspase-dependent and caspase-independent pathways. *Carcinogenesis* 28(10):2227–2235
- Reddivari L, Vanamala J, Safe SH, Miller JC Jr (2010) The bioactive compounds alpha-chaconine and gallic acid in potato extracts decrease survival and induce apoptosis in LNCaP and PC3 prostate cancer cells. *Nutr Cancer* 62(5):601–610
- Revina TA, Speranskaya AS, Kladnitskaya GV, Shevelev AB, Valueva TA (2004) Subtilisin protein inhibitor from potato tubers. *Biochemistry (Moscow)* 69(10):1092–1098
- Revina TA, Kladnitskaya GV, Gerasimova NG, Gvozdeva EL, Valueva TA (2010) Protein trypsin inhibitor from potato tubers. *Biochemistry (Moscow)* 75(1):36–40
- Reyes LF, Miller JC, Cisneros-Zevallos L (2005) Antioxidant capacity, anthocyanins and total phenolics in purple-and red-fleshed potato (*Solanum tuberosum* L.) genotypes. *Am J Potato Res* 82(4):271–277
- Robert L, Narcy A, Rock E, Demigne C, Mazur A, Rémésy C (2006) Entire potato consumption improves lipid metabolism and antioxidant status in cholesterol-fed rat. *Eur J Nutr* 45:267–274
- Robert L, Narcy A, Rayssiguier Y, Mazur A, Rémésy C (2008) Lipid metabolism and antioxidant status in sucrose vs. potato-fed rats. *J Am Coll Nutr* 27(1):109–116
- Roddick JG, Rijnbergen AL, Weissenberg M (1990) Membrane-disrupting properties of the steroidal glycoalkaloids solasonine and solamargine. *Phytochemistry* 29(5):1513–1518
- Rodriguez-Saona LE, Giusti MM, Wrolstad RE (1998) Anthocyanin pigment composition of red-fleshed potatoes. *J Food Sci* 63:458–465
- Roumeliotis E, Kloosterman B, Oortwijn M, Kohlen W, Bouwmeester HJ, Visser RG, Bachem CW (2012) The effects of auxin and strigolactones on tuber initiation and stolon architecture in potato. *J Exp Bot* 63(12):4539–4547
- Rydberg U, Andersson R, Aman P, Larsson H (2001) Comparison of starch branching enzyme I

- and II from potato. Eur J Biochem 268(23):6140–6145
- Rytel E (2012) Changes in the levels of glycoalkaloids and nitrates after the dehydration of cooked potatoes. Am J Potato Res 89(6):501–507
- Rytel E, Goubowska G, Lisinska G, Peksa A, Aniolowski K (2005) Changes in glycoalkaloid and nitrate contents in potatoes during French fries processing. J Sci Food Agric 85:879–882
- Rytel E, Tajner-Czopek A, Aniolowska M, Hamouz K (2013) The influence of dehydrated potatoes processing on the glycoalkaloids content in coloured-fleshed potato. Food Chem 141(3):2495–2500
- Rytel E, Tajner-Czopek A, Kita A, Aniolowska M, Kucharska AZ, Sokół-Łętowska A, Hamouz K (2014) Content of polyphenols in coloured and yellow fleshed potatoes during dices processing. Food Chem 161:224–229
- Saito K, Horie M, Hoshino Y, Nose N, Nakazawa H (1990) High-performance liquid chromatographic determination of glycoalkaloids in potato products. J Chromatogr A 508:141–147
- Salinas JP, Hartman TG, Karmas K, Lech J, Rosen RT (1994) Lipid-derived aroma compounds in cooked potatoes and reconstituted dehydrated potato granules. In: Ho CT, Hartman TG (eds) Lipids in food flavors. ACS symposium series, vol 558, Chapter 8, pp 108–129, ACS Publications, Washington DC
- Samarin AM, Poorazarang H, Hematyar N, Elhamirad A (2012) Phenolics in potato peels: extraction and utilization as natural antioxidants. World Appl Sci J 18(2):191–195
- Sanches-Silva A, Lopez-Hernández J, Paseiro-Losada P (2005) Profiling flavor compounds of potato crisps during storage using solid-phase microextraction. J Chromatogr A 1064(2):239–245
- Sapers GM (1970) Flavor quality in explosion puffed dehydrated potato. 2. Flavor contribution of 2-methylpropanal, 2-methylbutanal and 3-methylbutanal. J Food Sci 35(6):731–733
- Sapers GM, Sullivan JF, Talley FB (1970) Flavor quality in explosion puffed dehydrated potato. 1. A gas chromatographic method for the determination of aldehydes associated with flavor quality. J Food Sci 35(6):728–730
- Sapers GM, Osman SF, Dooley CJ, Panasiuk O (1971) Flavor quality of explosion puffed dehydrated potato. 3. Contribution of pyrazines and other compounds to the toasted off-flavor. J Food Sci 36(1):93–95
- Sapers GM, Panasiuk O, Talley FB, Osman SF, Shaw RL (1972) Flavor quality and stability of potato flakes. Volatile components associated with storage changes. J Food Sci 37(4):579–583
- Sapers GM, Panasiuk O, Talley FB, Shaw RL (1974) Flavor quality and stability of potato flakes: effects of drying conditions, moisture content and packaging. J Food Sci 39(3):555–558
- Schieber A, Saldaña MDA (2009) Potato peels: a source of nutritionally and pharmacologically interesting compounds – a review. Food 3(2):23–29
- Schreiber K, Osske G (1962) Isolierung von cycloartenol aus blättern der kulturkartoffel *Solanum tuberosum* L. sterine und triterpenoide. II. Mitteilung. Kulturpflanze 10:372–383
- Schreiber K, Osske G (1963) Isolierung von 4 α -methyl-5 α -stigmasta-7,24(28)-dien-3 β -ol aus *Solanum tuberosum* sowie über die identität dieser verbindung mit α 1. sterine und triterpenoide. III. Mitteilung. Experientia 19:69–71
- Schreiber K, Osske G (1964) Über die 4 α -Mmethyl-Sterine der kartoffelpflanze *Solanum tuberosum* L. sterine und triterpenoide. V. Mitteilung. Tetrahedron 20(11):2575–2584
- Schreiber K, Osske G, Sembdner G (1961) Identifizierung von β -sitosterin als hauptsterin des kartoffelkäfers (*Leptinotarsa decemlineata* Say). Experientia 17:463–464
- Schreiber L, Franke R, Hartmann K (2005) Wax and suberin development of native and wound periderm of potato (*Solanum tuberosum* L.) and its relation to peridermal transpiration. Planta 220(4):520–530
- Schütz S, Weissbecker B, Koch UT, Hummel HE (1999) Detection of volatiles released by diseased potato tubers using a biosensor on the basis of intact insect antennae. Biosens Bioelectron 14:221–228
- Schwall GP, Safford R, Westcott RJ, Jeffcoat R, Tayal A, Shi YC, Gidley MJ, Jobling SA (2000) Production of very-high-amylose potato starch by inhibition of SBE A and B. Nat Biotechnol 18(5):551–554
- Schwartz JJ, Wall ME (1955) Isolation of the sterols of the white potato 1, 2. J Am Chem Soc 77(20):5442–5443
- Self R, Swain T (1963) Flavour in potatoes. Proc Nutr Soc 22(2):176–182
- Self R, Rolley HLJ, Joyce AE (1963) Some volatile compounds from cooked potatoes. J Sci Food Agric 14(1):8–14
- Serra O, Hohn C, Franke R, Prat S, Molinas M, Figueras M (2010) A feruloyl transferase involved in the biosynthesis of suberin and suberin-associated wax is required for maturation and sealing properties of potato periderm. Plant J 62(2):277–290
- Shakya R, Navarre DA (2006) Rapid screening of ascorbic acid, glycoalkaloids, and phenolics in potato using high-performance liquid chromatography. J Agric Food Chem 54(15):5253–5260
- Shakya R, Navarre DA (2008) LC-MS analysis of solanidane glycoalkaloid diversity among tubers of four wild potato species and three cultivars (*Solanum tuberosum*). J Agric Food Chem 56(16):6949–6958
- Shih MJ, Kuć J (1974) α and β -solanarine in Kennebec *Solanum tuberosum* leaves and aged tuber slices. Phytochemistry 13(6):997–1000
- Shim EH, Choung SY (2014) Inhibitory effects of *Solanum tuberosum* L. var. vitelotte extract on 2,4-dinitrochlorobenzene-induced atopic dermatitis in mice. J Pharm Pharmacol 66(9):1303–1316
- Shimoi T, Ushiyama H, Kan K, Saito K, Kamata K, Hirokado M (2007) Survey of glycoalkaloids content in the various potatoes. Shokuhin Eiseigaku Zasshi 48(3):77–82 (in Japanese)

- Silva EM, Simon PW (2005) Genetic, physiological, and environmental factors affecting acrylamide concentration in fried potato products. *Adv Exp Med Biol* 561:371–386
- Sinden SL, Webb RE (1972) Effect of variety and location on the glycoalkaloid content of potatoes. *Am Potato J* 49(9):334–338
- Singh N, Rajini PS (2008) Antioxidant-mediated protective effect of potato peel extract in erythrocytes against oxidative damage. *Chem Biol Interact* 173(2):97–104
- Singh N, Kamath V, Rajini PS (2005a) Attenuation of hyperglycemia and associated parameters in STZ-induced diabetic rats by dietary supplementation of potato peel powder. *Clin Chim Acta* 353(1–2):166–175
- Singh N, Kamath V, Rajini PS (2005b) Protective effect of potato peel powder in ameliorating oxidative stress in streptozotocin diabetic rats. *Plant Foods Hum Nutr* 60(2):49–54
- Sizer CE, Maga JA, Craven CJ (1980) Total glycoalkaloids in potatoes and potato chips. *Agric Food Chem* 28(3):578–579
- Slack EB (1948) Nitrogenous constituents of the potato. *Nature* 161(4084):211–212
- Smith DB, Roddick JG, Jones JL (1996) Potato glycoalkaloids: some unanswered questions. *Trends Food Sci Technol* 7(4):126–131
- Smith DB, Roddick JG, Jones JL (2001) Synergism between the potato glycoalkaloids alpha-chaconine and alpha-solanine in inhibition of snail feeding. *Phytochemistry* 57(2):229–234
- Soh NL, Brand-Miller J (1999) The glycaemic index of potatoes: the effect of variety, cooking method and maturity. *Eur J Clin Nutr* 53(4):249–254
- Sotelo A, Serrano B (2000) High-performance liquid chromatographic determination of the glycoalkaloids alpha-solanine and alpha-chaconine in 12 commercial varieties of Mexican potato. *J Agric Food Chem* 48(6):2472–2475
- Spelbrink RE, Lensing H, Egmond MR, Giuseppin ML (2015) Potato patatin generates short-chain fatty acids from milk fat that contribute to flavour development in cheese ripening. *Appl Biochem Biotechnol* 176:231–243
- Stanković M, Ostojica tojanović O, Kobilarov N (1990) Unsaponifiable lipids from haulm and tuber sprouts of potato (*Solanum tuberosum* L.). *Potato Res* 33(4):459–464
- Stegemann H, Loeschcke V (1961) The proteins in the potato tuber. *Landw Forsch* 14:269–272
- Stevens LH, Davelaar E (1996) Isolation and characterization of blackspot pigments from potato tubers. *Phytochemistry* 42(4):941–947
- Stevens LH, Davelaar E (1997) Biochemical potential of potato tubers to synthesize blackspot pigments in relation to their actual blackspot susceptibility. *J Agric Food Chem* 45:4221–4226
- Stushnoff C, Ducreux LJ, Hancock RD, Hedley PE, Holm DG, McDougall GJ, McNicol JW, Morris J, Morris WL, Sungurtas JA, Verrall SR, Zuber T, Taylor MA (2010) Flavonoid profiling and transcriptome analysis reveals new gene-metabolite correlations in tubers of *Solanum tuberosum* L. *J Exp Bot* 61(4):1225–1238
- Subrahmanyam M (1996) Honey dressing versus boiled potato peel in the treatment of burns: a prospective randomized study. *Burns* 22(6):491–493
- Sukhova LS, Macháčková I, Eder J, Bibik ND, Korableva NP (1993) Changes in the levels of free IAA and cytokinins in potato tubers during dormancy and sprouting. *Biol Plant* 35(3):387–391
- Sun Y, Jiang LZ, Wei DX (2013) Partial characterization, in vitro antioxidant and antiproliferative activities of patatin purified from potato fruit juice. *Food Funct* 4(10):1502–1511
- Suttle JC (1995) Postharvest changes in endogenous ABA levels and ABA metabolism in relation to dormancy in potato tubers. *Physiol Plant* 95(2):233–240
- Suttle JC (1998a) Involvement of ethylene in potato microtuber dormancy. *Plant Physiol* 118(3):843–848
- Suttle JC (1998b) Postharvest changes in endogenous cytokinins and cytokinin efficacy in potato tubers in relation to bud endodormancy. *Physiol Plant* 103(1):59–69
- Suttle JC (2004a) Involvement of endogenous gibberellins in potato tuber dormancy and early sprout growth: a critical assessment. *J Plant Physiol* 161(2):157–164
- Suttle JC (2004b) Physiological regulation of potato tuber dormancy. *Am J Potato Res* 81(4):253–262
- Suttle JC, Hultstrand JF (1994) Role of endogenous abscisic acid in potato microtuber dormancy. *Plant Physiol* 105(3):891–896
- Szafranek BM, Synak EE (2006) Cuticular waxes from potato (*Solanum tuberosum*) leaves. *Phytochemistry* 67(1):80–90
- Tajner-Czopek A, Rytel E, Kita A, Pęksa A, Hamouz K (2012) The influence of thermal process of coloured potatoes on the content of glycoalkaloids in the potato products. *Food Chem* 133(4):1117–1122
- Tajner-Czopek A, Rytel E, Aniolkowska M, Hamouz K (2014) The influence of French fries processing on the glycoalkaloid content in coloured-fleshed potatoes. *Eur Food Res Technol* 238(6):895–904
- Tateo F, Bononi M, Gallone F (2010) Acrylamide content in potato chips on the Italian market determined by liquid chromatography tandem mass spectrometry. *Int J Food Sci Technol* 45:629–634
- The Plant List (2014) *Solanum tuberosum* L. www.the-plantlist.org/
- Thorne HV, Clarke GF, Skuce R (1985) The inactivation of herpes simplex virus by some Solanaceae glycoalkaloids. *Antiviral Res* 5(6):335–343
- Toma RB, Orr PH, D'Appolonia B, Dintzis FR, Tabekhia MM (1979) Physical and chemical properties of potato peel as a source of dietary fiber in bread. *J Food Sci* 44(5):1403–1407
- Tömösközi-Farkas R, Daoud HG, Polgar Z, Hajos G (2006) Determination of glycoalkaloids in Hungarian potatoes by HPLC. *Chromatographia* 63:S115–S118
- Tudela JA, Cantos E, Espín JC, Tomás-Barberán FA, Gil MI (2002) Induction of antioxidant flavonol biosynthesis in fresh-cut potatoes. Effect of domestic cooking. *J Agric Food Chem* 50(21):5925–5931

- Ugent D (1968) The potato in Mexico: geography and primitive culture. *Econ Bot* 22:108–123
- Ulrich D, Hoberg E, Neugebauer W, Tiemann H, Darsow U (2000) Investigation of the boiled potato flavors by human sensory and instrumental methods. *Am J Potato Res* 77:111–117
- Uppal DS (1987) Varietal and environmental effect on the glycoalkaloid content of potato (*Solanum tuberosum* L.). *Plant Foods Hum Nutr* 37(4):333–340
- U.S. Department of Agriculture, Agricultural Research Service (USDA-ARS) (2014) USDA national nutrient database for standard reference, release 27. Nutrient Data Laboratory Home Page. <http://www.ars.usda.gov/ba/bhnrc/ndl>
- USFDA (2008) Acrylamide: information on diet, food storage, and food preparation. <http://www.fda.gov/Food/FoodborneIllnessContaminants/ChemicalContaminants/ucm151000.htm>
- Valueva TA, Revina TA, Mosolov VV (1997) Potato tuber protein proteinase inhibitors belonging to the Kunitz soybean inhibitor family. *Biochemistry (Mosc)* 62(12):1367–1374
- Valueva TA, Revina TA, Kladnitskaya GV, Mosolov VV (1998) Kunitz-type proteinase inhibitors from intact and *Phytophthora*-infected potato tubers. *FEBS Lett* 426(1):131–134
- Valueva TA, Revina TA, Kladnitskaya GV, Mosolov VV, Mentel P (1999) Primary structure of a 21-kD protein from potato tubers. *Biochemistry (Mosc)* 64(11):1258–1265
- Van Gelder WMJ, Van Vinke JH, Scheffer JJC (1988) Steroidal glycoalkaloids in tubers and leaves of *Solanum* species used in potato breeding. *Euphytica* 48:147–158
- van Koningsveld GA, Gruppen H, de Jongh HH, Wijngaards G, van Boekel MA, Walstra P, Voragen AG (2001) Effects of pH and heat treatments on the structure and solubility of potato proteins in different preparations. *J Agric Food Chem* 49(10):4889–4897
- Van Staden J (1976) The nature of a cytokinin in potato tubers. *Potato Res* 19(3):249–252
- Varns JL, Glynn MT (1979) Detection of disease in stored potatoes by volatile monitoring. *Am Potato J* 56(4):185–197
- Varns JL, Shaw R (1973) An internal standard for rapid analysis of potato sugars by gas chromatography. *Potato Res* 16(3):183–184
- Verbist JF, Monnet R (1979) A propos de la teneur en solanine des petits tubercules nouveaux de pomme de terre (*Solanum tuberosum* L.). The solanine content of small new tubers of potato (*Solanum tuberosum* L.). *Potato Res* 22:239–244
- Verde Méndez Cdel M, Rodríguez Delgado MA, Rodríguez Rodríguez EM, Díaz Romero C (2004) Content of free phenolic compounds in cultivars of potatoes harvested in Tenerife (Canary Islands). *J Agric Food Chem* 52(5):1323–1327
- Verma SC, Purohit LK, Sharda RT, Purohit AN, Upadhyay MD (1972) Anthocyanin in dark- and light-grown sprouts of potato. *Potato Res* 15(2):166–169
- Vinson JA, Demkosky CA, Navarre DA, Smyda MA (2012) High-antioxidant potatoes: acute in vivo antioxidant source and hypotensive agent in humans after supplementation to hypertensive subjects. *J Agric Food Chem* 60(27):6749–6754
- Visser JH, Avé DA (1978) General green leaf volatiles in the olfactory orientation of the Colorado beetle, *Leptinotarsa decemlineata*. *Entomol Expt Appl* 24(3):738–749
- Visser JH, Van Straten S, Maarse H (1979) Isolation and identification of volatiles in the foliage of potato, *Solanum tuberosum*, a host plant of the Colorado beetle, *Leptinotarsa decemlineata*. *J Chem Ecol* 5(1):13–25
- Wagih ME, Wiersema SG (1996) *Solanum tuberosum* L. In: Flach M, Rumawas F (eds) Plant resources of South-East Asia, no. 9. Plants yielding non-seed carbohydrates. Prosea Foundation, Bogor, Indonesia, pp 148–154
- Waglay A, Karboune S, Alli I (2014) Potato protein isolates: recovery and characterization of their properties. *Food Chem* 142:373–382
- Wagner R, Grosch W (1997) Evaluation of potent odorants of French fries. *LWT-Food Sci Technol* 30(2):164–169
- Wagner RK, Grosch W (1998) Key odorants of French fries. *J Am Oil Chem Soc* 75(10):1385–1392
- Wang S, Panter KE, Gaffield W, Evans RC, Bunch TD (2005) Effects of steroidal glycoalkaloids from potatoes (*Solanum tuberosum*) on in vitro bovine embryo development. *Anim Reprod Sci* 85(3–4):243–250
- Wang QY, Chen Q, He ML, Mir P, Su JY, Yang Q (2011) Inhibitory effect of antioxidant extracts from various potatoes on the proliferation of human colon and liver cancer cells. *Nutr Cancer* 63(7):1044–1052
- Wang C, He XW, Huang Q, Fu X, Luo FX, Li L (2013) Distribution of octenylsuccinic substituents in modified A and B polymorph starch granules. *J Agric Food Chem* 61(51):12492–12498
- Waterer DR, Pritchard MK (1984) Monitoring of volatiles: a technique for detection of soft rot (*Erwinia carotovora*) in potato tubers. *Can J Plant Pathol* 6:165–171
- Watson AA, Davies DR, Asano N, Winchester B, Kato A, Molyneux RJ, Stegelmeier BL, Nash RJ (2000) Calystegine alkaloids in the potato and other food plants. In: Tu AT, Gaffield W (eds) Natural and selected synthetic toxins: biological implications. American Chemical Society, Washington, DC, pp 129–139
- Weidel E, Schantz M, Richling E (2014) A rapid method for quantifying chlorogenic acid levels in potato samples. *J AOAC Int* 97(3):902–907
- Weissbecker B, Van Loon JJ, Posthumus MA, Bouwmeester HJ, Dicke M (2000) Identification of volatile potato sesquiterpenoids and their olfactory detection by the two-spotted stinkbug *Perillus bioculatus*. *J Chem Ecol* 26(6):1433–1445
- Whitfield FB, Last JH, Tindale CR (1982) Skatole, indole and p-cresol: components in off-flavoured frozen French fries. *Chem Ind* 17:662–663

- Wojnowska I, Poznanski S, Bednarski W (1981) Processing of potato protein concentrates and their properties. *J Food Sci* 47(1):167–172
- Wood FA, Young DA (1974) TGA in potatoes. Canada Department of Agriculture, Ottawa. Publication no 153
- Woolfe JA, Poats SV (1987) Potato in the human diet. Cambridge University Press, Cambridge, 231 pp
- Wu ZG, Xu HY, Ma Q, Cao Y, Ma JN, Ma CM (2012) Isolation, identification and quantification of unsaturated fatty acids, amides, phenolic compounds and glycoalkaloids from potato peel. *Food Chem* 135(4):2425–2429
- Xu XY, Li WD, Lu ZH, B T, Hydamaka AW (2009) Phenolic content, composition, antioxidant activity, and their changes during domestic cooking of potatoes. *J Agric Food Chem* 57(21):10231–10238
- Xue HL, Bi Y, Wei JM, Tang YM, Zhao Y, Wang Y (2013) New method for the simultaneous analysis of types A and B trichothecenes by ultrahigh-performance liquid chromatography coupled with tandem mass spectrometry in potato tubers inoculated with *Fusarium sulphureum*. *J Agric Food Chem* 61(39):9333–9338
- Xue HL, Bi Y, Tang YM, Zhao Y, Wang Y (2014) Effect of cultivars, *Fusarium* strains and storage temperature on trichothecenes production in inoculated potato tubers. *Food Chem* 151:236–242
- Yan B, Stark RE (2000) Biosynthesis, molecular structure, and domain architecture of potato suberin: a (13) C NMR study using isotopically labeled precursors. *J Agric Food Chem* 48(8):3298–3304
- Ye HQ, Miao YT, Zhao CC, Yuan Y (2011) Acrylamide and methylglyoxal formation in potato chips by microwaving and frying heating. *Int J Food Sci Technol* 46(9):1921–1926
- Yoshida M, Ono H, Chuda Y, Yada H, Ohnishi-Kameyama M, Kobayashi H, Ohara-Takada A, Matsuura-Endo C, Mori M, Hayashi N, Yamaguchi Y (2005) Acrylamide in Japanese processed foods and factors affecting acrylamide level in potato chips and tea. *Adv Exp Med Biol* 561:405–413
- Yoshihara T, Omer EA, Koshino H, Sakamura S, Kikuta Y, Koda Y (1989) Structure of a tuber-inducing stimulus from potato leaves (*Solanum tuberosum* L.). *Agric Biol Chem* 53(10):2835–2837
- Yu DQ, Liu YD, Fan BF, Klessig DF, Chen ZX (1997) Is the high basal level of salicylic acid important for disease resistance in potato? *Plant Physiol* 115(2):343–349
- Zaidul ISM, Yamauchi H, Takigawa S, Matsuura-Endo C, Suzuki T, Noda T (2007) Correlation between the compositional and pasting properties of various potato starches. *Food Chem* 105(1):164–172
- Zhao XC, Sheng F, Zheng JL, Liu RT (2011) Composition and stability of anthocyanins from purple *Solanum tuberosum* and their protective influence on Cr(VI) targeted to bovine serum albumin. *J Agric Food Chem* 59(14):7902–7909
- Zia-ur-Rehman HF, Shah WH (2004) Utilization of potato peels extract as a natural antioxidant in soy bean oil. *Food Chem* 85(2):215–220
- Zitnak A (1961) The occurrence and distribution of free alkaloid solanidine in netted gem potatoes. *Can J Biochem Physiol* 39(8):1257–1265
- Zitnak A (1981) Photoinduction of glycoalkaloids in cured potatoes. *Am Potato J* 58(8):415–421
- Zitnak A, Johnston GR (1970) Glycoalkaloid content of B514-6 potatoes. *Am Potato J* 47(7):256–260

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