Review

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Health-beneficial properties of potato and compounds of interest

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Abstract

Potatoes have shown promising health-promoting properties in human cell culture, experimental animal and human clinical studies, including antioxidant, hypocholesterolemic, anti-inflammatory, antiobesity, anticancer and antidiabetic effects. Compounds present such as phenolics, fiber, starch and proteins as well as compounds considered antinutritional such as glycoalkaloids, lectins and proteinase inhibitors are believed to contribute to the health benefits of potatoes. However, epidemiological studies exploring the role of potatoes in human health have been inconclusive. Some studies support a protective effect of potato consumption in weight management and diabetes, while other studies demonstrate no effect and a few suggest a negative effect. As there are many biological activities attributed to the compounds present in potato, some of which could be beneficial or detrimental depending on specific circumstances, a long-term study investigating the association between potato consumption and diabetes, obesity, cardiovascular disease and cancer while controlling for fat intake is needed.

Keywords: potatoes; consumption; functional compounds; antinutritional compounds; beneficial effects

INTRODUCTION

Potato (*Solanum tuberosum* L.) belonging to the family Solanaceae is a nourishing food that is rich in calories and biologically active phytochemicals such as β-carotene, polyphenols, ascorbic acid, tocopherol, α-lipoic acid, selenium and dietary fiber.[1] The main nutrient in potato is the storage polysaccharide starch. When consumed in whole food form, the energy density of potato is similar to that of legumes.[2] Potatoes are an inexpensive source of energy and good quality protein.[3] Historically, this was the typical Irish diet, which provided all the important vitamins and nutrients required to support a better life than any other crop when eaten as the sole article of diet.[4]

Potato production has significantly increased in recent years in many countries, especially in Asia where it has become more important as a food and industrial crop.[2] In terms of production, potato ranks sixth in the world after sugar cane, maize, rice, wheat and milk (http://faostat3.fao.org/browse/rankings/commodities_by_regions/E). Until the early 1990s, most potatoes were grown and consumed in Europe, North America and countries of the Soviet Union. Since then, there has been a dramatic increase in potato production and demand in Asia and Africa, where output rose from less than 26 million tons in the early 1960s to more than 217 million tons in 2013. In 2009, world production of potatoes exceeded 334 million tons, and according to FAO data, world production has increased up to approximately 376 million tons in 2013 (http://faostat3.fao.org/browse/rankings/commodities_by_regions/E). Asia and Europe are the world's major potato-producing regions, accounting for more than 80% of world production in 2013 (http://faostat3.fao.org/browse/rankings/commodities_by_regions/E). The per capita consumption of potato is very high in European countries (87.8 kg year^{-1}). Though Asia is the largest producer in the world, the per capita consumption of potato was only 23.9 kg year^{-1} in 2005 (http://www.fao.org/potato-2008/en/world/index.html). Potato consumption in Asia is on the increase, and the demand for potato in Asia is expected to double or triple over the next few years.[2] Although people in Asia are traditionally dependent upon cereals and are generally unaware of the nutritional value of potatoes, in many countries, potatoes are a very significant part of the diet and can make a significant contribution to human nutrition.

In addition to the starch content, potato tubers are rich in proteins, carbohydrates, minerals, vitamins and especially bioactive compounds that contribute to the health-beneficial properties of potato.[2] Phytochemicals in potato are concentrated in its peel, and their content is higher in cultivars with brighter peel colors.[5] Phytochemicals play an important role in human health as antioxidants, and the high daily consumption of potato contributes to a high phenolic content in our diet.[6] Since the fat content of potato is low, consumption of potato instead of other high-carbohydrate foods such as rice and pasta may potentially benefit our overall health.[7] Potato has been suggested as a potential functional food by several authors owing to the presence of several antioxidant compounds in abundant quantities.[1,2,8]

On the contrary, potatoes are also reported to be unhealthy and are often maligned in nutrition because of their suspected link to

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obesity.[7] This is the reason why their Economic Research Service (ERS) data for per capita availability (PCA) of vegetables, a proxy for vegetable consumption, show that vegetable consumption, including consumption of white potatoes, has declined in the past decade.[9] Though the fat content and energy density of potato are similar to those of legumes, potato is thought to contain more calories and fat compared with rice.[2] Some food guides do not include potatoes in the vegetable group because of their association with high-fat diets.[7] To change this negative trend, it is important to point out the nutritionally important components of potato tubers, including bioactive compounds such as polyphenols and carotenoids. Consumption of potato in the right amount with low fat, as opposed to its usual form of French fries or potato chips, could potentially lead to the prevention of oxidation-linked chronic diseases such as type II diabetes and cardiovascular diseases.[2] Therefore this review will mainly focus on discussing the functional properties of potatoes and their link in preventing the development of chronic diseases.

POTATO AND HEALTH: COMPOUNDS OF INTEREST

Several authors have reviewed the health benefits of potatoes.[2,8,10] Potatoes which were assumed to play an important role in the development of chronic diseases in the western world were found to exert many health-promoting properties. The beneficial properties exerted by the tubers are reported to be due to the presence of compounds such as phenolics, anthocyanins, resistant starch, dietary fiber, potato proteins, etc.[2] Compounds such as glycoalkaloids and lectins which were considered as antinutritional compounds were also found to exert some health-promoting properties.[11,12] Therefore this part of the review will briefly discuss some of the compounds which are reported to contribute to the health-promoting properties of potato.

Phenolic compounds

Phenolic acids and polyphenols play an important role in human health. Though potatoes are not considered as a food item with high antioxidant activity, the tubers actually present a very significant source of antioxidants in our daily diet owing to their high daily consumption.[1] Potatoes are reported to be the third most important source of phenols after apples and oranges.[13] Phenolic acids and flavonoids are the most prominent phytochemical groups present in potato.[10] Chlorogenic acid and caffeic acid are the two main phenolic acids present in potato, followed by protocatechuic acid, *trans*-cinnamic acid, *p*-coumaric acid, ferulic acid, vanillic acid, gallic acid, syringic acid and salicylic acid.[14] Most of the phenolic acids in potato are present between the cortex and the peel of the potato tuber, and their content reduces towards the center of the tuber.[15]

Chlorogenic acid is the predominant phenolic acid (>90%) found in potatoes, ranging from 3 to 90 mg per 100 g fresh weight (FW) in flesh and from 100 to 400 mg per 100 g FW in peel.[10] Chlorogenic acid is reported to play an important role against the development of diabetes[16] and hypertension[17] and has also been reported to exhibit several desirable anticarcinogenic properties.[18,19] Chlorogenic acid has strong antioxidant activity and potatoes are an excellent source of this. This partially explains the protective role of potatoes against the development of many chronic diseases.

After chlorogenic acid, caffeic acid is the second most abundant phenolic acid present in potato, ranging from 310 to 420 μg per 100 g FW.[14] There is a huge variation in the chlorogenic acid content of potatoes based on variety. The chlorogenic acid and caffeic acid content in pigmented cultivars is greater than that in non-pigmented cultivars. Stushnoff *et al.*[20] found an approximately 10-fold difference in the chlorogenic acid content of pigmented and non-pigmented cultivars and a 100-fold difference in caffeic acid content.[21] The cultivars Vitelotte and Luminella were reported to have the highest polyphenol contents (5202 and 572 μg g^{-1} dry weight (DW) respectively in outer flesh), whereas Charlotte and Bintje had the lowest contents (19.5 and 48.0 μg g^{-1} DW) respectively.[22] The yellow PORO3PG6-3 and purple PORO4PG82-1 cultivars had the highest concentration of total phenolics, 2-fold greater than in the white cultivar Russet Burbank.[23] However, in contrast, in a study done by Al-Saikhan *et al.*,[24] total phenolics were found to be dependent on genotype and not on flesh color.

Anthocyanins

Anthocyanins belonging to the flavonoid group are present in high amounts in pigmented potatoes.[1] Anthocyanins play an important role in human health and are reported to show antioxidant,[25,26] anticancer[27] and anti-inflammatory[28] activities. The anthocyanin content in potatoes has been reported to range between 5.5 and 35 mg per 100 g FW.[2] Generally, purple and red flesh cultivars contain higher amounts of polyphenols than cultivars with a cream or white flesh.[23,29] The total anthocyanin content in red flesh potato ranged from 6.9 to 35 mg per 100 g FW and that in purple flesh potato from 5.5 to 17.1 mg per 100 g FW.[1] Andre *et al.*[30] observed an 11-fold variation in the total phenolic content of Andean potato landraces, and the dark purple flesh tubers from the Andean cultivar 704429 contained exceptionally high levels of total anthocyanins (16.33 mg g^{-1} DW). In a study done by Hamouz *et al.*,[29] the purple flesh varieties Blaue Elise, Blaue St. Galler, Violette and Vitelotte and the red flesh varieties Herbie 26, Highland Burgundy Red, Rosalinde and Rote Emma were found to contain high amounts of anthocyanins in the range of 135.3–573.5 mg cyanidin kg^{-1} FW. Anthocyanin concentration extending up to 368 mg per 100 g FW was found in the purple flesh cv. Urenika.[31]

More than 98% of the total anthocyanins in potatoes are in acylated form, and many are acylated with *p*-coumaric acid and ferulic acid.[1] In colored potatoes, 3-rutinoside-5-glucoside and 3-rutinoside derivatives of pelargonidin, petunidin, malvidin, cyanidin, peonidin and delphinidin have been reported.[31–33] Red flesh potatoes contain pelargonidin- and peonidin-3-rutinoside-5-glycosides while purple flesh potatoes are rich in malvidin- and petunidin-3-rutinoside-5-glycosides acylated with *p*-coumaric and ferulic acid.[32,33] Eichhorn and Winterhalter[34] studied the major anthocyanins in four pigmented potato cultivars. Pelargonidin was found to be the only anthocyanidin in cv. Highland Burgundy Red, malvidin was the predominant aglycon of cv. Vitolette, and peonidin derivatives were found only in cv. Shetland Black in minor amounts. Petunidin derivatives were detected in all varieties except Highland Burgundy Red.

Potato starch

Starch is the major storage polysaccharide in potato. Potatoes contain amylose and amylopectin in a ratio of 1:3 (w/w).[8] The amylose content of potato cultivars is approximately 31.2% while the content in wild species is 29.7% of the total starch.[2] Amylose is more resistant to digestion than amylopectin. Owing to the high amylose content, potato starch is generally resistant to the action of amylase and other amylolytic enzymes in the digestive tract, behaving as a resistant starch.[8] Raw potato starch was shown to be highly resistant to hydrolysis with pancreatic amylase *in vitro*.[35] The low digestibility of potato starches is due to the granule crystallinity, the smaller surface/volume ratio of the granules, and the presence of a layer of non-starch barrier material such as polysaccharides on the surface of starch granules.[36] However, cooking leads to a loss of crystallinity, thereby reducing the resistance to amylase digestion.[2] Cooling, freezing and drying make the starch partially resistant to amylase.

In addition to this, phosphorylated potato starches also add to the digestive resistance.[2] Potato starches are more highly phosphorylated than other cereal starches.[37] Potato starch was found to contain 0.2–0.4% (w/w) of monoesterified phosphate groups.[38] The phosphorus in potato starch is present primarily as phosphate esterified to the glucose residues of the starch.[39] Phosphate is bound only in the amylopectin fraction of the starch, and the glucosyl residues of amylopectin are phosphorylated at either the C6 or C3 position. Most phosphorylation occurs at the C6 position (70–80%), while only 20–30% occurs at the C3 position.[39] On average, one out of every 200–300 glucose units is reported to be phosphorylated.[40] Noda *et al.*[41] studied the phosphorus content of 69 potato cultivars and reported a range between 434 and 1087 $\mu g\ g^{-1}$. The lowest content was observed in Setoyutaka and the highest in Kachikei No. 11. In their study, the purple (Inca Purple, Kitamurasaki and Hokkai No. 92) and red (Inca Red and Hokkai No. 91) flesh potato cultivars were found to contain relatively higher levels of phosphorus (891–1065 $\mu g\ g^{-1}$). Resistant starch and phosphorylated starch in potatoes have been reported to contribute to blood glucose-lowering and cholesterol-lowering properties.[37,42] Enzymatically solubilized polysaccharides from potato pulp have been reported to act as dietary fibers and prebiotics *in vitro*[43] and *in vivo*.[44]

Glycoalkaloids

Glycoalkaloids are nitrogen-containing steroidal glycosides. The primary glycoalkaloids in potato are α-solanine and α-chaconine, which make up 95% of total glycoalkaloids.[12] The other glycoalkaloids found are β- and γ-solanine, β- and γ-chaconine, α- and β-solamarine, demissidine and 5-β-solanidan-3-α-ol in cultivated potatoes and leptines, commersonine, demissine and tomatine in wild potatoes.[3] At certain levels, these compounds may be toxic to bacteria, fungi, viruses, insects, animals and even humans. This toxic effect occurs only when glycoalkaloid intake is very high.[45] The maximum established level for potato glycoalkaloids is 20 mg per 100 g FW. However, the glycoalkaloid content of the majority of potato cultivars is between 3 and 10 mg per 100 g of tubers.[45] In addition to their known toxic effects, studies during the past 10 years suggest that glycoalkaloids may also possess beneficial effects, including anticancer,[46,47] antimalarial, anti-inflammatory and antiglycemic[2] effects, depending on the dose and conditions of use.

Potato fiber

Dietary fiber plays an important role in human health by acting as a bulking agent and increasing the intestinal mobility and hydration of feces, binding unwanted materials such as carcinogenic and mutagenic substances, facilitating digestion and acting as a growth medium for beneficial intestinal microflora and is reported to exert hypoglycemic, hypocholesterolemic and anticancer effects.[48–51] The European Prospective Investigation on Cancer study reported that the protective effect exerted by fiber against colorectal cancer and other health problems was irrespective of the fiber source.[52]

Dietary fiber in potatoes is made of cellulose, hemicelluloses, pectins, lignin and other substances that are resistant to digestive enzymes.[53] In the UK, next to cereals and vegetables, potatoes are the main contributor of dietary fiber in all age groups of men and women.[52] Dietary fiber makes up approximately 2.5% of fresh tuber mass and is concentrated in the peel, with approximately 50% of potato peel being dietary fiber.[48] According to Buttriss and Stokes,[52] the non-starch polysaccharide content or dietary fiber content of baked potato with and without skin was 2.7 and 1.4 g per 100 g FW respectively.

Cooking, cooling and storage of potatoes are reported to produce retrograded starch.[52] Microwave heating and deep-fat frying of potatoes were found to reduce the amount of *in vitro* digestible starch and significantly increase both resistant starch and water-insoluble dietary fiber, while the soluble dietary fiber content was unchanged.[54] Soluble dietary fibers are reported to decrease the rate of gastric emptying and intestinal transit time, thereby slowing down the rate of digestion and glucose absorption by the intestine through forming viscous solutions.[36] Potato is a good source of the water-soluble dietary fiber pectin, which is almost completely metabolized by colonic bacteria.[55] Baking and extrusion cooking increased the non-starch polysaccharides in potato peel, while the soluble/insoluble dietary fiber ratio in the peel was increased only in the latter.[55] Varo *et al.*[56] reported that heat-treated potato samples contained more water-insoluble dietary fiber and less starch than raw samples.

The addition of viscous dietary fiber to a carbohydrate meal reduces the glycemic response of the meal.[57] Lightowler and Henry[57] investigated mashed potatoes containing 1, 2 or 3% (w/w) of high-viscosity hydroxypropylmethylcellulose, a modified cellulose dietary fiber, and observed a significant reduction in glycemic responses in all samples compared with standard mashed potato. Dietary fiber preparations from potato skin and flesh were tested for their ability to adsorb the hydrophobic mutagen 1,8-dinitropyrene (DNP) *in vitro*. Potato skin walls were found to strongly adsorb DNP, whereas the flesh walls of potato adsorbed only a small proportion of DNP and a large increase in the proportion of DNP was found in solution.[58]

Potato protein and peptides

The major groups of potato proteins present in potato tuber are patatins, protease inhibitors and other proteins.[59] Patatin has been shown to possess antioxidant activity and also inhibit hydroxyl radical-induced DNA damage *in vitro*.[24,60–62] Since peptides have lower molecular weights and less complex structures than proteins, their solubility, digestibility and absorbability are higher than those of proteins.[63] Peptides isolated from potato protein have been reported to exhibit antioxidant,[63] anticancer,[64] antiobesity,[65] antihyperlipidemic[66] and antifungal/antibiotic[67] activities and were also reported to exhibit angiotensin-converting enzyme (ACE) inhibition *in vitro*.[68]

Potato protease inhibitors

Protease inhibitors (PIs) represent approximately 50% of the total amount of proteins in potato juice.[69] The most studied protease inhibitors from potato tuber are potato protease inhibitor I (PI-1), potato protease inhibitor II (PI-2) and potato carboxypeptidase inhibitor (PCI).[69] Although PIs were considered as antinutritional compounds, they have regained interest in recent years because

Table 1. Functional properties and physiological effects of potato compounds

Active ingredient	Functional properties	Physiological effects	References
Phenolic compounds	Antioxidant	Prevent oxidative damage to DNA and other biomolecules; up-regulate expression of cellular antioxidant enzymes	2,24
	Antidiabetic	Reduce gut glucose absorption; increase insulin sensitivity; inhibit hepatic glucose-6-phosphatase; reduce oxidative stress and overall food intake	2,16,99,116
	Antihypertensive	Reduce systolic and diastolic blood pressure; inhibit angiotensin-converting enzyme (ACE)	8,142
	Anticancer	Prevent proliferation of cancer cells; up-regulate expression of cellular antioxidant enzymes; block inflammatory mediators linked to cancer; suppress ROS-mediated NF-*k*B, AP-1 and MAPK activation	18,19,75,133
	Antiobesity	Inhibit lipid metabolism through down-regulation of expression of p38 mitogen-activated protein kinase (MAPK) and uncoupled protein 3 (UCP-3); suppress adipogenesis	74,99
Anthocyanins	Antioxidant	Prevent oxidative damage to DNA; prevent lipid oxidation; up-regulate expression of cellular antioxidant enzymes	25,28,80,82
	Anticancer	Suppress proliferation and elevate apoptosis; induce mitochondrial release and nuclear uptake of proapoptotic Endo G and AIF proteins; cytotoxic effect against cancer cell lines	130,131,134
	Anti-inflammatory	Reduce plasma concentrations of CRP, 8-hydrodeoxyguanosine and IL-6	28
Potato starch	Hypoglycemic	Reduce glycemic response of food	115
(resistant and phosphorylated starch)	Hypolipidemic	Resist digestion; increase fecal bile acid excretion; inhibit synthesis of fatty acids; increase cecal short-chain fatty acid synthesis	37,42,143
Glycoalkaloids	Anticancer	Reduce metastasis and induce apoptosis; inhibit proliferation; reduce matrix metalloproteinase-2 (MMP-2) and MMP-9 activity; cytotoxic to cancer cells	12,46,47,135,136
	Anti-inflammatory	Reduce interleukin-2 (IL-2) and IL-8 production; reduce NO production	121
Lectins	Anticancer	Induce apoptosis; limit synthesis of proteins, DNA and RNA in cancer cells	2,11
Fiber	Hypoglycemic	Reduce glycemic response of food; reduce hypertrophy of liver and kidney; normalize activity of antioxidant enzymes	116
	Hypocholesterolemic	Bind to bile acid and reduce availability; increase cecal short-chain fatty acid synthesis; increase neutral steroid excretion	49,123
	Anticancer	Prevent tumor cell proliferation; reduce cancer cell motility; induce apoptosis; cause morphological changes in tumor cells; adsorb mutagens	50,51,58,123
Potato protein and peptides	Antioxidant	Prevent oxidative damage to DNA and other biomolecules	60,63,87
	Antiobesity	Induce CCK release/enhance response; stimulate CCK1R expression in enteroendocrine cells; inhibit luminal proteases	65,71,92,96,98
	Antihyperlipidemic	Increase fecal bile acid and neutral steroid excretion; inhibit cholesterol absorption through suppression of micellar solubility of cholesterol;	46,122,128
	Antihypertensive	increase cecal short-chain fatty acid synthesis Inhibit ACE	59,68,141
Potato protease inhibitors	Anticancer	Prevent tumor cell proliferation and H_2O_2 formation; block UV-induced activation of AP-1	64,69
	Antiobesity	Enhance release of CCK and reduce food intake; enhance response to CCK primarily by inhibition of trypsin-like proteolytic activity	65,70,71,92

of their exerted anticancer[64] and antiobesity[70] activities. PIs have been reported to show anticancer activity by preventing tumor cell proliferation and H_2O_2 formation and by protecting from the effects of solar UV irradiation.[69] They act as satiety agents by enhancing the release of cholecystokinin.[71]

METABOLIC EFFECTS

Potatoes have received much interest recently owing to their observed biological effects *in vitro*, such as free radical scavenging,[72,73] modulation of enzymatic activity[74] and inhibition of cellular proliferation.[18,51,75] There is an extensive literature describing each of these biological properties (Table 1). We have focused on the biological effects of potatoes, including their antioxidant, antiobesity, antidiabetic, anticancer, anti-inflammatory, antihyperlipidemic and antihypertensive activities, which are commonly ascribed to help explain their potential role against the development of non-communicable diseases such as cardiovascular disease, type 2 diabetes mellitus (T2D), cancer, etc.

Antioxidant activity

Health-promoting properties such as antidiabetic, antithrombotic, anticancer, antimutagenic, anti-inflammatory and antiallergic activities of plant extracts result from powerful antioxidant and free radical-scavenging properties of phenolic compounds.[72,73,76] Potato tubers are one of the richest sources of antioxidants in the human diet. For example, in the USA, among all fruits and vegetables consumed, potatoes ensure an average daily intake of about 64 mg polyphenols per capita.[1] The main potato antioxidants are polyphenols (1.226–4.405 mg kg^{-1}), ascorbic acid (170–990 mg kg^{-1}), carotenoids (as high as 4 mg kg^{-1}), tocopherols (0.5–2.8 mg kg^{-1}), selenium (0.01 mg kg^{-1}) and α-lipoic acid.[1] Chlorogenic acid is the primary phenolic compound (being more than 90% of phenolics) found in potatoes.[10,22,77] In a US study, the total phenolic content of peeled potato was 28 mg per 100 g FW and it was ranked 20th out of 23 commonly consumed vegetables and was ranked ninth in terms of antioxidant activity.[78] Flavonoid and flavone extracts from potatoes show high scavenging activities toward oxygen radicals.[79]

Potato chlorogenic acid has been found to be an effective inhibitor of lipid oxidation.[24] Antioxidant capacity has been directly related to anthocyanin content in potatoes.[25] Hypercholesterolemic rats fed 300 g of purple potato flakes experienced significantly lower thiobarbituric acid-reactive substance (TBARS) levels in the serum and liver and antioxidant enzyme activities in the liver than those in the control and white potato groups.[80] The serum urate levels in all flake groups were significantly lower than that in the control group. An extract from purple potato (Hokkai No. 91) ameliorated galactosamine-induced liver damage in rats[81] and was suggested to show hepatoprotective effects via inhibition of lipid peroxidation and/or inflammation in rats. Red potato flakes improved the antioxidant system by enhancing the expression of hepatic superoxide dismutase mRNA in rats.[82]

Potato peel extracts (PPEs) possess strong antioxidant activity. Almost 50% of phenolics are located in the peel and adjoining tissues, while the level decreases toward the center of the tuber.[15] Probably owing to the strong antioxidant activity of anthocyanins, extracts prepared from red peels have stronger activity than those from brown peels.[83] PPE inhibited lipid peroxidation induced by $FeSO_4$ and ascorbic acid in rat red blood cells (RBCs) and human RBC membranes with similar effectiveness (80–85% inhibition) at a concentration of 2.5 mg mL^{-1}.[73] Scanning electron microscopy results demonstrated that PPE significantly protected rat RBCs against H_2O_2-induced morphological changes and inhibited oxidative damage to human erythrocytes. Additionally, some studies have reported the use of potato peel as a source of antioxidant for the prevention of oxidation of meat products,[84] soy bean oil[85] and fish oil.[86]

Potato protein hydrolysate has demonstrated potent antioxidant activity *in vitro* and *in vivo*.[63,87] Intact and hydrolyzed potato proteins lowered the production of peroxide and TBARS values in beef, and hydrolyzed potato protein reduced oxidant-induced biochemical changes of pork myofibril protein isolate.[88] Three peptides (5A, 5C and 6C) purified from potato protein hydrolysate fractions inhibited linoleic acid oxidation and lipid oxidation in the erythrocyte membrane, and oral administration of the peptides reduced ethanol-induced gastric mucosal damage in rats.[63]

Antiobesity activity

From 1991 to 1999, Schulze *et al.*[89] examined the association between dietary patterns and weight gain in women enrolled in the Nurse's Health Study II. The western dietary pattern (included red and processed meats, refined grains, sweets and desserts, and potatoes) was associated with weight gain, while the prudent dietary pattern (included fruits, vegetables, whole grains, fish, poultry and salad dressing) facilitated weight maintenance. Mozaffarian *et al.*[90] followed up on the Schulze *et al.*[89] study and evaluated weight gain in 4 year intervals between 1986 and 2006 in three separate prospective cohorts. Participants gained weight with an increase in the intake of potato chips, fried potatoes, sugar-sweetened beverages and unprocessed and processed meats. Anyhow, the two prospective cohort studies did not consider the effect of the fat consumed along with potato, which can also contribute to weight gain.

Potato proteinase inhibitor II (PI2) reduced food intake in humans when administered orally.[65,70] At a 1.5 g dose before a meal, PI2 reduced energy intake in healthy subjects,[65] while an average 2 kg weight loss was demonstrated in overweight women when PI2 was taken daily prior to lunch and dinner for 4 weeks.[91] PI2 has been reported to enhance the release of cholecystokinin (CCK), which induces satiety.[71,92] CCK is a natural signaling peptide released by the gut in response to food. Once released, CCK acts on various target organs, resulting in signals to the brain, where it induces feeling of fullness and satiety.[65,93]

Several studies have shown that intact proteins or their hydrolysates could stimulate the secretion of CCK from enteroendocrine cells.[94–97] A potato extract (Potein) containing 60% (w/w) carbohydrate and 20% (w/w) protein, including trypsin-inhibitory proteins, was examined for its effect on food intake and CCK secretion in enteroendocrine cells in rats.[71] Oral administration of the extract was found to suppress food intake and stimulate CCK secretion by direct stimulation of enteroendocrine cells and through inhibition of luminal trypsin. In contrast, in another study, feeding of a crude potato PI concentrate was suggested to enhance CCK response, primarily by inhibition of trypsin-like proteolytic activity in the small intestine and not by direct stimulation of CCK-producing cells.[92] The potato extract (Potein) included proteins other than trypsin inhibitors and other non-protein components. Thus the presence of some of these components might be responsible for the direct stimulation of CCK secretion. It is likely that CCK secretion is the result of both the direct action of an active compound on CCK-producing cells and luminal protease inhibition *in vivo*.[98]

Yoon *et al.*[74] studied the antiobesity mechanism of a new purple potato variety in Sprague-Dawley rats. The rats were fed a high-fat diet (HFD) with ethanol extract of *S. tuberosum* L. cv. Bora Valley (ESTBV). ESTBV showed potential antiobesity activity via inhibition of lipid metabolism through down-regulating the expression of p38 mitogen-activated protein kinase (MAPK) and uncoupled protein 3 (UCP-3). In a study done by Kubow *et al.*,[99] both sexes of C57BL/6J mice were fed a high-fat diet (HFD) for 10 weeks with and without polyphenolic-rich potato extract (PRPE) of cultivars Onaway and Russet Burbank. PRPE attenuated weight gain in male and female mice by as much as 63.2 and 55.75% respectively. The reduced body weight gain in mice treated with PRPE was mostly due to reduction in adiposity. These results demonstrated greater potency of weight reduction than reported for the anthocyanin-rich extract of purple flesh potatoes in HFD-fed rats.[74]

Pharmacological treatment of obesity has become widely used in most countries, although the number of available drugs are still very limited. The FDA-approved antiobesity drugs orlistat and sibutramine are widely used and have been reported to show a weight loss of <5 kg in 1–4 year randomized, placebo-controlled trials.[100] PI-2 found in potatoes is commercially available for weight loss applications (e.g. Slendesta, Suprx™, Sola thin). Clinical trials indicate that PI-2 is a safe and effective natural agent that promotes satiety and healthy weight loss. When consumed as recommended, potato extract has resulted in statistically significant weight loss and reductions in waist and hip measurements.[101]

Antidiabetic effect

The glycemic index (GI) of a food depends on the carbohydrate source and amount, the degree of starch gelatinization and the type and amount of fiber present.[8] Potato is a carbohydrate-rich crop cultivated widely around the world. The GI value of potatoes and potato products varies widely based on the cultivar, maturity, starch structure, processing and storage conditions.[36] According to published literature, the GI values of potatoes range from very low, i.e. 23–41, in unspecified cultivars of potatoes grown in Africa, India and Romania[102] to as high as 144 in boiled Desiree.[103] The GI value of boiled red potatoes (consumed cold), baked US Russet potatoes, instant mashed potatoes and boiled red potatoes was 56, 77, 88 and 89 respectively.[104] Henry *et al.*[105] examined the GI values of eight varieties of commercially available potatoes in Great Britain and reported a range from 56 to 94. In addition, some wild cultivars grown in Australian Aboriginal regions are reported to exhibit lower GI values than the commercially grown potato cultivars in the western world.[36] Based on available studies, potato is the food which yields the most variable glycemic response. However, despite all these facts, potatoes as a whole are categorized as a high-GI food, which requires reconsideration.

In a study done by Montonen *et al.*,[106] potatoes consumed along with butter and whole milk were reported to be associated with increased risk of T2D. Fried potatoes were found to be associated with increased risk of T2D in both men and women.[107] Data from the Nurse's Health Study reported a positive association between intake of potatoes and diabetes risk in obese women. It was found that substituting one serving of potatoes per day for one serving of whole grains increased the risk of T2D by 30%.[108]

In contrast, potato intake was found to be associated with a lower risk of T2D in the Shanghai Women's Health Study, where rice was found to increase the risk.[109] The contradictory findings of these studies were explained based on a relatively low intake of potato in the Chinese population and the lower amounts of fat added to potatoes during the cooking process by Chinese women. Some other reports also show an inverse relationship between potato intake and risk of T2D,[110,111] and some studies also found no association between potato intake and risk of T2D.[112–114]

To date, most studies on potato intake and diabetes have focused on a potential positive association. Anyhow, digestibility of raw uncooked potato starch was reported to be poor compared with that of most cereal starches: in the raw state, 87% of potato starch resists digestion, while cereal starches are digested slowly but completely and absorbed *in vivo*.[115] In addition, PPEs, which are rich in polyphenolic antioxidants, were reported to reduce hyperglycemia, oxidative stress and overall food intake in diabetic rats.[116] Potatoes are rich in chlorogenic acid and caffeic acid which are implicated in the prevention of T2D.[117] Chlorogenic acid slows down the release of glucose into the blood stream[16] and hence could be helpful in lowering the GI of potatoes. More studies are needed to confirm the link between potato dietary fiber and polyphenolic content in prevention or therapy for T2D; also, development of potato cultivars with high resistance to digestion will open up a new avenue for low-GI potatoes which would be a good source for diabetic patients and may even decrease the risk of T2D.

Anti-inflammatory effect

Markers of systemic inflammation include C-reactive protein (CRP) and the pro-inflammatory cytokine interleukin-6 (IL-6). Data from subjects (age ≥ 6 years) participating in the 1999–2000 and 2001–2002 National Health and Nutrition Examination Survey (NHANES) showed an association between consumption of whole plant foods, including potatoes, and lower CRP levels.[118] The ethanolic extract of potato tubers significantly inhibited both carrageenan- and formalin-induced inflammation in mice as well as arachidonic acid-induced ear edema in mice.[119] In the Busselton Health Study, when the body mass index (BMI) was controlled, potato intake was associated with lower CRP levels.[120] In the first human study to investigate the effects of potato consumption on inflammation, Kaspar *et al.*[28] showed that pigmented potatoes were anti-inflammatory and lowered plasma concentrations of CRP, 8-hydrodeoxyguanosine and IL-6 in healthy men compared with men fed a white potato diet. In a recent study, potato glycoalkaloids and PPEs were found to possess anti-inflammatory properties *in vitro*.[121]

Antihyperlipidemic effect

There is some evidence that potato protein,[66,122] resistant and phosphorylated starch,[37,42] potato fiber,[50,123] glycoalkaloids[124] and phenolic compounds[15] contribute to the cholesterol-lowering properties of potato. Rats fed a potato-enriched diet for 3 weeks had lower plasma cholesterol and triglycerides and reduced liver cholesterol compared with control rats.[123] In another rat feeding study, Robert *et al.*[125] compared the effects of potato-, starch- and sucrose-based diets on lipid metabolism. Compared with starch and sucrose diets, consumption of cooked potatoes for 3 weeks lowered cholesterol and triglycerides and enhanced the antioxidant status and short-chain fatty acids in the potato-fed animals.

Some studies have reported the positive effect of raw potato starch on plasma and liver lipids.[126,127] Unlike gelatinized potato starch, raw potato starch is resistant to digestion and acts as dietary fiber in the digestive tract. Retrograded starch from two varieties of potato pulp lowered serum total cholesterol and triglyceride levels compared with controls.[42] Rats fed Benimaru potato showed reduced cholesterol levels and higher levels of fecal bile acids, while rats fed Hokkaikogane potato exhibited reduced triglyceride concentrations and lower hepatic mRNA levels of fatty acid synthase and sterol regulatory element-binding protein-1c (SREBP-1c).[42] Potato starches are naturally highly phosphorylated, which possibly avoids attack by digestive enzymes and controls serum lipids.[42] Gelatinized potato starch containing a high level of phosphate was found to reduce serum free fatty acids and triglycerides and liver triglycerides.[37] Potato starch increased fecal bile acid excretion but had no effect on cecal short-chain fatty acid synthesis or pH. Thus the lipid-lowering properties were suggested to be due to slow digestion of gelatinized high-phosphorus potato starch and not due to the cecal fermentation-promoting properties of resistant starch.[37]

Compared with soy and casein, feeding potato protein to rats resulted in reduced serum total cholesterol, increased fecal bile acid and neutral steroid excretion.[128] The lipid-lowering property was related to the relatively lower methionine content and methionine/glycine ratio in potato protein. Lower concentrations of plasma cholesterol and low-density lipoprotein (LDL) were also reported in pigs fed potato protein for 3 weeks.[129] Liyanage *et al.*[122] studied the hypocholesterolemic effect of potato peptides. Rats fed a cholesterol-free diet containing 20% (w/w) potato peptides showed greater serum high-density lipoprotein (HDL) cholesterol and fecal steroid output and less non-HDL cholesterol. The results were attributed to inhibition of cholesterol absorption, possibly via suppression of micellar solubility of cholesterol. In another study where hypercholesterolemia was induced in rats, potato peptides reduced the serum non-HDL cholesterol level by stimulating fecal steroid excretion, accelerated by cecal short-chain fatty acids.[66]

Whole potato is a rich source of dietary fiber. Camire *et al.*[49] evaluated the bile acid-binding ability of potato peels *in vitro*. All peels bound a smaller percentage of bile acids than did the drug cholestyramine. Extrusion cooking of peel enhanced the binding of cholic, deoxycholic and glycocholic acids, and binding of deoxycholic acid was highly correlated with total dietary fiber and insoluble dietary fiber content. Feeding of potato peel reduced plasma total cholesterol in rats.[50,123] The authors ascribed the hypolipidemic activity to its fiber content. However, it is likely that the polyphenol content and other antioxidants[15] as well as glycoalkaloids contributed to the observed hypocholesterolemia, since both tomato and potato glycoalkaloids have a strong affinity for cholesterol.[124]

Anticancer effect

Several studies have shown a reduction in proliferation of cancer cells when treated with potato extracts.[18,51,75,130] Phenolic acids, anthocyanins, fiber, glycoalkaloids and proteinase inhibitors identified in potatoes have been implicated in the suppression of cancer cell proliferation *in vitro*[64,131–133] and *in vivo*.[27,134] Commercially available potato fiber extract (Potex) was reported to exhibit antiproliferative effect in several tumor cell cultures.[51] The fiber extract decreased cancer cell motility, induced apoptosis and also caused morphological changes in tumor cells.[51] Colored flesh potatoes are a rich source of anthocyanins with a wide array of health benefits.[1] Purple flesh potatoes were reported to suppress proliferation and elevate apoptosis of colon cancer cells compared with white and yellow flesh potatoes.[130] Anthocyanins in steamed purple and red potatoes suppressed the growth of benzopyrene-induced stomach cancer in mice.[134]

Extracts from four specialty potatoes and the anthocyanin fraction from genotype CO112F2-2 showed potent antiproliferative properties by increasing the levels of cyclin-dependent kinase inhibitor p27 in both androgen-dependent (LNCaP) and androgen-independent (PC-3) prostate cancer cell lines.[131] The anthocyanin fraction of the potato extract induced mitochondrial release and nuclear uptake of the proapoptotic Endo G and AIF proteins. *Solanum jamesii* tuber extracts showed antiproliferative and cytotoxic effects against HT-29 human colon cancer and LNCaP human prostate cancer cell lines.[133] Red pigmented Mountain Rose cultivar, rich in chlorogenic acid derivatives and anthocyanins, showed greater inhibition of carcinogenesis in rats with chemically induced breast cancer as compared with white Russet Burbank cultivar.[27]

Potato polyphenols are effective against human liver, colon and prostate cancer cells.[75,133] Studies with individual phenolics suggested that chlorogenic acid may be the primary compound responsible for the antiproliferative activity. In JB6 mouse epidermal cell line, chlorogenic acid suppressed the proliferation of A549 human lung cancer cell lines and blocked UVB- or TPA-induced transactivation of AP-1 and NF-*k*B, which are inflammatory mediators linked to cancer.[18] Proliferation of colon cancer cells and liver cancer cells *in vitro* was significantly inhibited by chlorogenic acid.[75]

Several studies have reported that potato glycoalkaloids exhibit an inhibitory effect on the growth of human cancer cell lines such as human colon (HT29), liver (HepG2), cervical (HeLa), lymphoma (U937) and stomach cancer cells.[135,136] α-Chaconine was found to be more effective than α-solanine.[136] α-Chaconine reduced lung cancer metastasis *in vitro* by suppression of the phosphoinositide 3-kinase (PI3K)/Akt/NF-*k*B signaling pathway[132] and induced apoptosis in HT-29 human colon cancer cells through caspase-3 activation and inhibition of ERK 1/2 phosphorylation.[137] In another study, α-chaconine and gallic acid in potato extracts were reported to decrease survival and induce apoptosis in LNCaP and PC3 prostate cancer cells.[47] However, in a recent study, potato glycoalkaloids were reported to show poor apoptotic activity, although the cytotoxic effect was equal to that of certain cancer drugs.[12] In addition to this, other compounds such as potato lectin[11,138] and potato protease inhibitors 1 and 2 were also reported to show anticancer activity.[64]

Antihypertensive effect

High potassium intake is associated with reduced blood pressure (BP). Potatoes are rich in potassium and very low in sodium.[8] Vinson *et al.*[139] studied the effect of potatoes on blood pressure in 18 overweight, hypertensive adult subjects for 4 weeks in a cross-over design. Consumption of purple potatoes reduced systolic and diastolic BP compared with baseline. Proteins isolated from potatoes and potato products exhibit ACE-inhibitory action. ACE inhibitors prevent the body from producing angiotensin II, a substance that affects the cardiovascular system by narrowing the blood vessels and releasing hormones that can raise BP.[140] Autolysis of protein isolates from potato tuber tissue was found to enhance ACE inhibition.[141] Pihlanto *et al.*[68] reported that hydrolysis of potato proteins increased their ACE-inhibitory potency. Potato tuber liquid, a by-product of the potato starch industry, was found to be a valuable source of ACE-inhibitory peptides.[59] The results of these studies suggest that potato may be a source for bioactive compounds that benefit cardiovascular health.

SUMMARY

Potato is a nutrient-dense food that provides significant amounts of nutrients without adding too many calories. In populations where potato is the staple food, potatoes are an important source of starch, phenolic compounds and dietary fiber (when eaten with the skin). Potatoes possess specific properties that benefit human health in various ways. Potato protein, peptides, protease inhibitors, phenolic compounds, anthocyanins, dietary fiber, resistant starches and phosphorylated starches have been reported to improve lipid profile, blood glucose level and blood pressure. *In vitro* and *in vivo* studies also suggest that anthocyanins, glycoalkaloids and lectins from potatoes are anticancer agents. However, as discussed, the *in vitro* and *in vivo* data have produced conflicting results on the association of potato consumption with obesity and development of diabetes. The data from epidemiological studies regarding these matters are far from convincing. However, to clearly understand the impact of potatoes on human health, a long-term study investigating the association between potato consumption and diabetes, obesity, cardiovascular disease and cancer while controlling for fat intake is needed. More information on the bioavailability of phenolic compounds in potatoes is also needed.

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