

The Potato in the Human Diet: a Complex Matrix with Potential Health Benefits

Christelle M. Andre • Sylvain Legay •
Christian Iammarino • Johanna Ziebel • Cedric Guignard •
Yvan Larondelle • Jean-Francois Hausman • Danièle Evers •
Lisa Miranda Miranda



Received: 17 November 2014 / Accepted: 22 November 2014 /
Published online: 18 February 2015
© European Association for Potato Research 2015

Abstract Beyond providing energy through its high starch content, the potato tuber can make a significant contribution to the dietary intake of certain minerals including potassium, phosphorous, magnesium and iron, as well as of vitamin C, dietary fibres and phenolic compounds. While some animal and human studies have shown beneficial associations between the consumption of potato, or some of its components, and health, some other studies could not confirm these positive effects. Numerous factors may indeed influence (i) the composition of the potato tuber itself, i.e. genotype, environmental conditions during growth, post-harvest storage conditions, cooking and processing, and (ii) the bioaccessibility and bioavailability of its components, affecting the final bioactivity. The purpose of this paper is to provide a brief overview of potato composition variability followed by an analysis of potential health-promoting effects and bioavailability of specific components including iron and phenolic compounds. It appeared that the various components of the potato matrix might interact with each other at the intestinal level, leading to favourable or detrimental effects on their bioavailability. The consumption of a potato cultivar with a high level of phenolic compounds may improve the health status of an individual regarding its risk of developing chronic diseases on the one hand, but may reduce iron absorption on the other hand, putting an individual at risk of micronutrient deficiency. Tailoring potato varieties or products to match the population nutritional needs appears therefore of major importance.

C. M. Andre (✉) • S. Legay • C. Iammarino • J. Ziebel • C. Guignard • J.-F. Hausman • D. Evers
Luxembourg Institute of Science and Technology, Department of Environmental Research and
Innovation, 5, avenue des Hauts-Fourneaux, L-4362 Esch/Alzette, Luxembourg
e-mail: christelle.andre@list.lu

Y. Larondelle • L. M. Miranda
Institut des Sciences de la Vie, Université catholique de Louvain, Croix du Sud, 2, boîte 8,
1348 Louvain-la-Neuve, Belgium

Keyword Bioavailability · Human health · Iron · Micronutrients · Nutritional value · Quality · Secondary metabolites · Vitamins

Introduction

Potato (*Solanum tuberosum* L.) is a crop native to the central Andean area of South America, but it is now cultivated and consumed in most parts of the world, with an average consumption in 2011 of 96 g/capita/day (FAO 2014). The overall nutritional value of potato is nowadays still greatly underestimated. Beyond providing energy through its high starch content, the potato tuber is an excellent source of proteins of high biological value and contains notable amounts of vitamin C, vitamin B6, vitamin B3, potassium, phosphorous, magnesium and iron. Potato is also a valuable source of health-promoting compounds in the human diet (Andre et al. 2007a, b). Understanding their role in human nutrition and, thereby, their effects on health requires knowledge on their chemistry, occurrence, bioaccessibility, bioavailability and biological properties. In this review, these aspects will be discussed, with a special emphasis on iron and bioactive secondary plant compounds including phenolic compounds.

Iron Content and Phytochemical Composition: A Strong Influence of the Genotype

Iron deficiency represents one of the most widespread forms of micronutrient malnutrition (Thompson 2007). Iron deficiency anaemia still persists worldwide, especially in countries where meat consumption and therefore heme iron intake is low. Iron deficiency during childhood and adolescence impairs physical and mental development. In adults, it reduces the capacity for physical work (WHO/FAO 2002). Biofortification of staple foods such as potato has tremendous potential to alleviate these deficiencies. Potato contains moderate amounts of (non-heme) iron, although due to their high consumption level, it may be considered as a valuable source of iron. Environmental growing conditions and the soil type in particular are strong determinants of iron concentrations in potato, although large genetic variations and inheritance patterns have been observed in the germplasm, indicating that breeding for increased iron content has also some potential (Anderson et al. 1999; Burgos et al. 2007; Haynes et al. 2012; Paget et al. 2014). Improved breeding and enriched mineral fertilisation are therefore alternative means to increase potato mineral status (White and Broadley 2005; Brown 2008). In peeled potato tubers, threefold to fourfold variations have been reported, with iron concentrations ranging from 9 to 37, 17 to 63 and 13 to 34 µg/g of dry weight in diverse cultivars grown in diverse locations in South America (Peru) (Burgos et al. 2007), USA (Brown et al. 2010) and Luxembourg (Fig. 1, unpublished results), respectively. However, determining the extent to which potato consumers will benefit from this iron content requires further knowledge on its bioaccessibility and bioavailability. Potato contains also a large number of phytochemicals that, although not all of them constituting essential nutrients, may positively or negatively affect

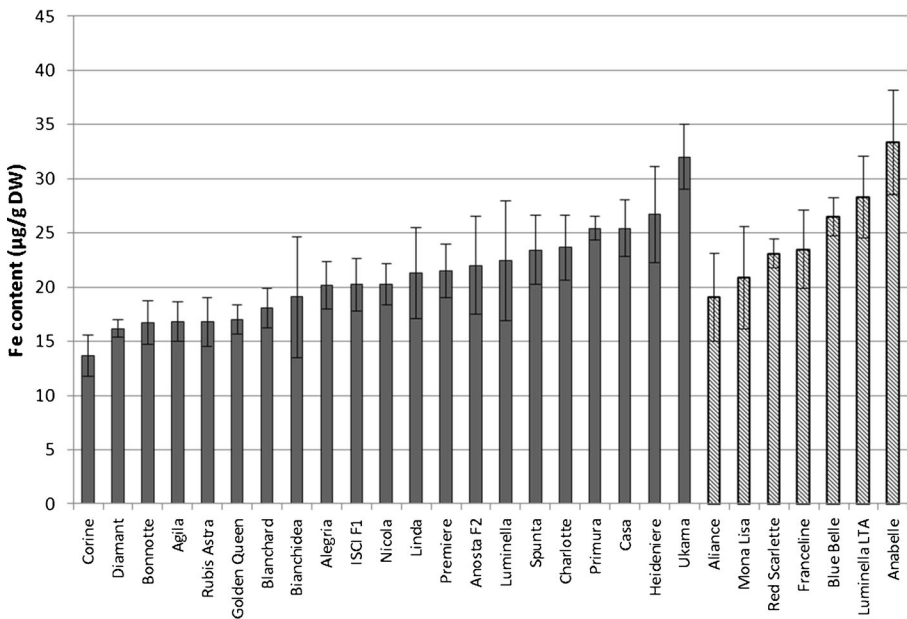


Fig. 1 Iron content in European cultivars harvested in 2012 in the north of Luxembourg (Binsfeld; fields—in grey and hashed bars—were 5 km apart). Data were obtained by inductively coupled plasma mass spectrometry (ICP-MS) as described in Lefèvre et al. (2012)

human health. Significant levels of hydrophilic antioxidants, i.e. phenolic compounds and vitamin C, and moderate levels of lipophilic carotenoids and vitamin E have been reported in potato (recently reviewed in Burlingame et al. (2009) and Ezekiel et al. (2013)). These phytochemical compounds have received much attention due to their prospective effects on the prevention of various chronic diseases such as cancers and cardiovascular and degenerative diseases (McCullough et al. 2012; Miller and Snyder 2012). The potato phenolic profile is dominated by chlorogenic acid and rutin, whereas lutein, violaxanthin, neoxanthin and zeaxanthin predominate the carotenoid pattern (Burgos et al. 2009a, b, c; Fernandez-Orozco et al. 2013). Wide genotypic variations exist in terms of phenolic composition, with a 72-fold variation reported for chlorogenic acid in the native germplasm (0.18–13 mg/g of dry weight) and the specific presence of anthocyanins in red or purple-skinned and purple-fleshed cultivars (Andre et al. 2007a, b). Furthermore, the phenolic distribution may vary within the potato tuber, with levels decreasing from the skin to the inner flesh (Deußner et al. 2012). Generally, purple- and red-fleshed cultivars contained higher amounts of total phenolic compounds than their white- or cream-fleshed counterparts. These coloured cultivars have also been associated with greater iron levels (Andre et al. 2007a, b; Brown 2008). Interestingly, accumulation of phenolic compounds was also noted in potato tubers exposed to an excess of iron (Chatterjee et al. 2006), suggesting an important role of phenolic compounds in reducing the oxidative stress potentially induced by iron. Similarly, a recent investigation on iron-biofortified black beans observed an increased level of phenolic compounds in the higher iron beans (Tako et al. 2014). However, further research would be needed to validate these observations.

Impact of Environmental Conditions

Environmental conditions during tuber development may influence the phytochemical production pathways and, thereby, the vitamin and bioactive composition of potato tubers. Experiments performed in two different highland environments could, however, confirm the stability of the ranking of some cultivars across harvest in terms of phenolic content (Andre et al. 2009a, b). Higher chlorogenic acid levels were found on warm locations with frequent periods of drought in comparison with locations of high-altitude climatic conditions (Hamouz et al. 2013). Higher amounts of both anthocyanins and total phenolics were also observed at locations with longer days and cooler temperatures (Reyes et al. 2004). Studies on the effects of the production system on the nutrient composition of potato tubers showed that potatoes produced in organic cultivation when compared with conventional cultivation contained higher or similar levels of phenolic compounds (Rosenthal and Jansky 2008; Søltoft et al. 2010). Literature data are, however, not consistent enough to conclude that potato tubers grown under organic farming contain higher amounts of phytochemicals.

Potato is adversely affected by environmental abiotic stresses, such as drought, high salinity and low temperature, as well as biotic stresses, such as pathogen infections. Interestingly, the phenylpropanoid pathway, leading to the production of phenolic compounds, is particularly affected when plants are exposed to such stresses (Dixon and Paiva 1995), as these can generate reactive oxygen species in plants, thereby causing oxidative stress and impacting the antioxidant responses. In particular, the impact of drought, one of the major limitations for sustainable agriculture worldwide, has been studied on the mineral and bioactive composition of potato. With regard to potato antioxidants, the responses to drought stress were complex with levels showing increases, decreases or remaining stable, depending on the genotype and the type of dietary antioxidant studied. A drastic reduction of anthocyanins and other phenolic compound was revealed in two red- and purple-fleshed cultivars, whereas an increase was shown in a purple-skinned and yellow-fleshed cultivar. Vitamin C contents were not affected by drought with the exception of the dark-purple-fleshed cultivar, in which the level was increased (Andre et al. 2009a, b). In a recent study, we also evaluated the influence of water depletion on the tuber mineral concentrations (expressed on dry weight basis) and showed an increase of most of the analysed elements (including iron) in most Andean cultivars under investigation (Lefèvre et al. 2012).

Post-harvest and Processing Effects

Once potato tubers are harvested, their “health value” can still be altered or improved through storage and processing. Even after harvest, in dormant tubers, metabolism remains active. Tubers start a process of aging, which is often associated with an increase of reactive oxygen species and oxidative stress (Coleman 2000). Accordingly, ascorbic acid endogenous levels in potato are not stable post-harvest, displaying shrinkages that can reach 25 to 65% of the initial values (Dale et al. 2003; Burgos et al. 2009a, b, c). Cold storage (4 °C) of potato tubers, which is associated with potato cold sweetening, i.e. increased concentration of sugars, has been shown to induce a rise of phenolic acid and anthocyanin concentrations (Lewis et al. 1999). Higher storage

temperatures may, however, inverse this tendency and result in non-affected or decreased phenolic contents, as described in Andre et al. (2009a, b).

Cooking and other processing methods may further modify the tuber composition in a genotype-dependent manner. Losses of iron during cooking of unpeeled tubers have been shown to be minimal (Burgos et al. 2007). When comparing different cooking methods of potatoes prepared with skin (baking, boiling, frying, microwaving), boiled samples were significantly lower in total carotenoid contents, whereas for total phenolics, increased contents were observed after baking, frying, and microwaving as compared to uncooked samples (Blessington et al. 2010). Boiling reduced the vitamin C concentration to a lesser extent than either baking or microwaving, with percentages of retention ranging from 53 to 97%, from 6 to 66% and from 6 to 39% in boiled, baked and microwaved potatoes, respectively. The losses may be caused by (i) leaching into cooking water, (ii) destruction by heat treatment and (iii) oxidation. Interestingly, the peel forms a barrier preventing loss of nutrients during cooking. As a consequence, boiling potato when peeled induces 10% additional losses of vitamin C or phenolic compounds as compared to boiling the tubers with the peel (Woolfe and Poats 1987; Barba et al. 2008). Generally, processing of potato lowers the levels of antioxidants to various extents (Kalt 2005). Traditional processing of potatoes to produce chuno, an Andean freeze-dried potato, resulted also in phenolic losses (Peñarrieta et al. 2011), whereas the iron level remained stable (Burgos et al. 2009a, b, c).

Bioaccessibility and Bioavailability Using In Vitro Models

Potato tubers contain interesting amounts of health-promoting components such as vitamin C, phenolic compounds and iron. However, numerous factors, as described above, may influence their composition before their consumption and thereby may modify their impact on human health. The story does not end here yet. The positive or negative effects of potato components on health will finally result either from interactions at the gastro-intestinal level (interactions with gastric or intestinal cells, with digestive enzymes or with the microflora in the large intestine) or from their presence in certain tissues, stressing the importance of determining their bioavailability, i.e. the proportion of the ingested substance that may be used by the target tissue, including aspects of absorption, metabolism and transport to the target organs. The capacity of the digestion process to release polyphenols from the food matrix (bioaccessibility) is yet the first step to determine their bioavailability.

The amount of phytochemicals that is released from the potato matrix during digestion and that is accessible for intestinal uptake (bioaccessibility) can be simulated by an in vitro gastro-intestinal digestion model. According to a recent study (Miranda et al. 2013), phenolic concentrations of potato tubers from two different varieties change during in vitro digestion. The concentrations of individual phenolic compounds are generally higher in gastric and in intestinal filtrate than in boiled potatoes, suggesting a release of the compounds from cell walls due to the action of diverse digestive enzymes or pH conditions. In vitro bioaccessibility of carotenoids from potato reveals that the gastric and the duodenal digestive stabilities of lutein and zeaxanthin in boiled tubers of the different accessions range from 70 to 95% (Burgos et al. 2013). The level of bioaccessible iron has, however, never been evaluated in potatoes. It is worth noting

that compounds or components not released during gastric and duodenal digestion may be further available in the colon thanks to the actions of the microflora.

Bioavailability of Phenolic Compounds

Bioavailability can be defined as the amount of a nutrient that can be absorbed and used for physiological function and/or storage. Knowledge on bioavailability is an essential prerequisite for determining bioactivity and impact on human health. Recent studies showed that more than 90% of dietary polyphenols are not directly bioavailable but are metabolised by the colonic microflora into bioavailable phenolic acids. The remaining 10% of polyphenols can be directly absorbed either through active transporters (for phenolic compound linked to glucose for instance) or passively thanks to their relatively high hydrophobicity (polyphenols in aglycone form). Once absorbed, polyphenols are extensively conjugated by glucuronidation, sulphation and methylation, which may radically change their biological activity (Clifford 2004). Therefore, concentrations of circulating polyphenols in their native form are reduced. The gastro-intestinal tract may, however, be exposed to concentrations much higher than in the circulation and direct effects of phenolic compounds are more likely to occur in this part (Stevenson and Hurst 2007). There is no specific intervention study on the bioavailability of phenolic compounds from potatoes. We, however, recently showed that about 0.3 to 0.9% of potato chlorogenic acid content is taken up by intestinal cells *in vitro* (Miranda et al. 2013), suggesting that most potato phenolic compounds are available for metabolism by the colonic microflora. Interestingly, it appears that numerous dietary factors may influence the bioavailability of phenolic compounds (recently reviewed in Bohn (2014)). The presence of divalent minerals in the food matrix, including iron, is likely to cause detrimental effects on phenolic compound bioaccessibility. The chelating property of phenolic compounds with iron appears therefore disadvantageous for the health benefits linked to both types of molecules, as described in the following section.

Bioavailability of Non-heme Iron

Interactions between iron and other compounds present in the human diet strongly determine the non-heme iron bioavailability. Therefore, non-heme iron absorption may be enhanced by simultaneous consumption of ascorbic acid, citric acid, meat and fish, whereas phytate, calcium and phenolic compounds may inhibit the absorption. Ferric iron (Fe(III)) must be first reduced to ferrous iron (Fe(II)) to be taken up by the divalent metal-ion transporter (DMT-1) (Gunshin et al. 1997). Intracellular iron concentration, storage and detoxification are further under the control of the ferritin protein, whereas ferroportin might have a role in iron release from intestinal cells. Potatoes contain significant amounts of vitamin C (ascorbic acid), contributing to about 20% of the dietary intake in Europe (Love and Pavek 2008). Ascorbic acid is a potent enhancer of iron uptake in humans. It reduces ferric iron (Fe(III)) to a ferrous (Fe(II)) form that is more absorbable by the cells. Recent studies revealed also that ascorbate plays a much more active role and may modulate iron metabolism by stimulating ferritin synthesis, inhibiting lysosomal ferritin degradation, decreasing cellular iron efflux and regulating Fe transport protein (transferrin) iron uptake (Lane and Richardson 2014). Phenolic

compounds may also influence iron uptake, through the formation of insoluble complexes with ferric iron in the gastrointestinal tract (Brune et al. 1989). Ferric iron is thought to bind to adjacent hydroxyls on galloyl and catechol groups of phenolic compounds. Chlorogenic acid, the predominant phenolic compound in potato (Andre et al. 2007a, b), is therefore able of forming chelates with ferric iron (Hynes and O’Coinceanainn 2004). By complexing iron, chlorogenic acid prevents it to act as a pro-oxidant through the Fenton and Haber–Weiss reactions (Lawen and Lane 2013) but also inhibits its absorption through intestinal cells and antagonises ascorbic acid action. Several studies have shown that beverages containing chlorogenic acid can inhibit the absorption of non-heme iron in man by up to 60% (Hurrell et al. 1999).

Quercetin-3-rutinoside (rutin), a flavonol from the flavonoid family, is the second most important polyphenol present in many potato cultivars (Andre et al. 2007a, b). Rutin has been shown to suppress free radical processes through scavenging reactive oxygen species and/or chelating iron, to an extent depending on pH conditions (Afanas’ev et al. 1989).

In a recent study performed by our group, differentiated Caco-2 TC7 cells (Chantret et al. 1994) were used to study iron bioavailability. These cells are derived from a human colorectal adenocarcinoma cell line. They undergo differentiation and polarisation and acquire characteristics of mature enterocytes: brush border membrane, tight junctions, expression of intestinal apical enzymes and transporters (Alvarez-Hernandez et al. 1994). In combination with simulated digestion, the Caco-2 cell model has been demonstrated to be effective in comparing iron bioavailability from diverse bean and maize genotypes (Glahn et al. 1998; Ariza-Nieto et al. 2007). Ferritin level in cells is a sensitive marker of iron uptake and enable measurement of iron availability in vitro (Glahn et al. 1998). Interestingly, we showed that, in contrast to chlorogenic acid, rutin led to an increased Fe(III) absorption by Caco-2 TC7 cells in a dose-dependent manner, as described for ascorbic acid (Fig. 2).

One explanation for the Fe(III) increased uptake by rutin could be that rutin acts as a hydrogen donating agent to Fe(III), leading thus to its reduction into Fe(II) (Zou et al. 2004) and allowing its uptake by DMT-1. Rutin is a quercetin with a rutinoside in position 3, and it is known that the quercetin-Fe(II) complex could be taken up via GLUT-1, a glucose transporter (Vlachodimitropoulou et al. 2011). A similar mechanism for rutin could be another way to explain the increased iron uptake in Caco-2 cells, although this has yet to be demonstrated. In addition, rutin slightly but significantly increased ferroportin gene expression in presence of iron (data not shown), suggesting that rutin in presence of iron could induce basolateral release of iron in the systemic circulation. Since ascorbic acid and rutin showed similar effects on iron uptake, it was interesting to study the combined effects of both compounds on iron uptake to highlight the mechanisms involved. At low concentrations, a combination of both compounds has a significant combined effect on Fe(III) absorption. At higher concentration of ascorbic acid, a plateau of ferritin level is reached, and there is no longer a combined effect of rutin (Fig. 3). This was probably due to a saturation of the system masking the impact of rutin on ferritin synthesis. It may indicate that the mechanisms leading to an increased ferritin synthesis by ascorbic acid and rutin are similar.

An overview model for the mechanism of iron uptake, storage and redistribution induced by ascorbic acid, chlorogenic acid and rutin in Caco-2 cells is suggested in

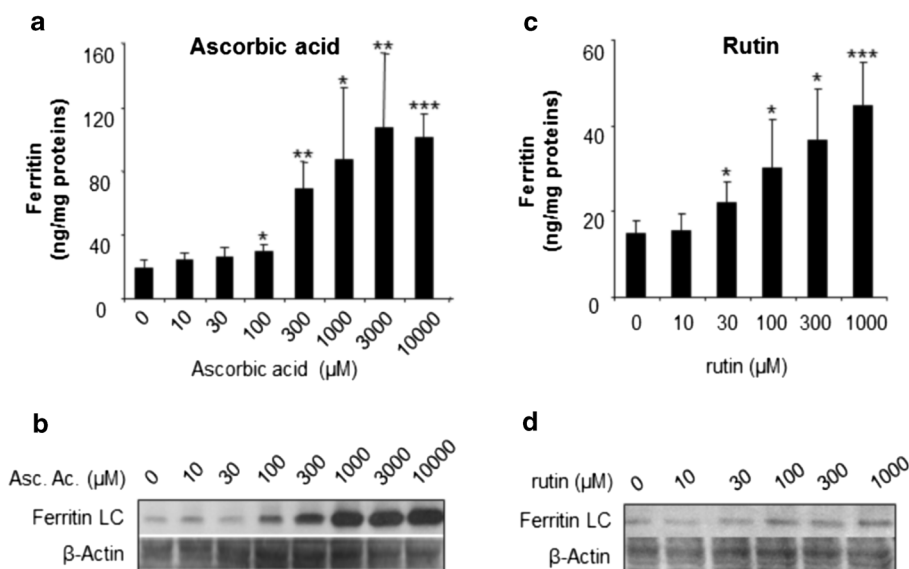


Fig. 2 Total ferritin expression induced by ascorbic acid (**a, b**) and rutin (**c, d**) treatments in Caco-2 TC7 cells. Cells were grown as previously described (Miranda et al. 2013). Briefly, they were treated with indicated amounts of ascorbic acid and 300 μM FeCl₃ or rutin and 300 μM FeCl₃. **a, c** Ferritin expression was evaluated by an ELISA assay and normalised using total protein concentration. Results are the mean of four independent assays ± SD, and they were assessed using a one-way ANOVA test with a Bonferroni post hoc test. * $p < 0.05$, ** $p < 0.01$ and *** $p < 0.001$ indicate a significant difference compared with the control. **b, d** shows an anti-Lc ferritin immunoblot with beta-actin as a loading control. The results shown are the most representative of the Western blots made from four independent assays

Fig. 4. Chlorogenic acid and rutin uptake by intestinal cells is very low, and probably most of the observed effects take place in the intestinal lumen and may be due to a chelation of iron by phenolic compounds. However, we cannot exclude that the small

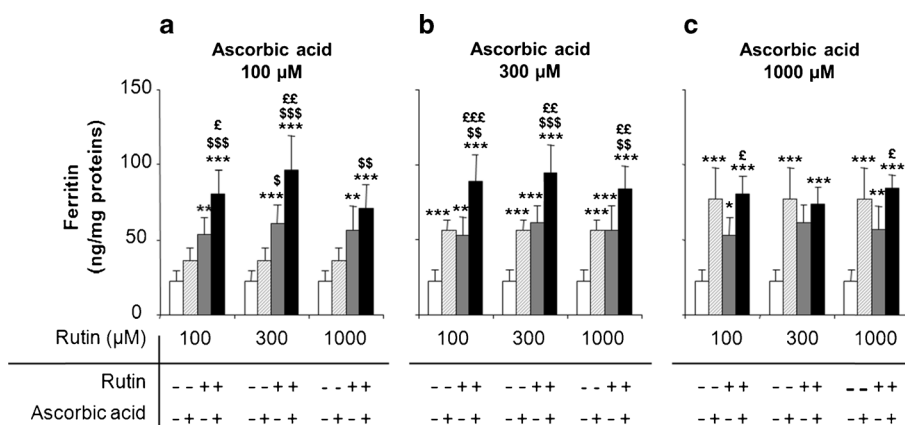


Fig. 3 Combined effects of ascorbic acid and rutin on total ferritin expression in Caco-2 cells. Caco-2 cells were treated with 300 μM FeCl₃, **a** 100 μM, **b** 300 μM or **c** 1000 μM ascorbic acid and/or rutin. Cells with 300 μM FeCl₃ only (white bars), ascorbic acid (hatched bars), rutin (grey bars) and rutin combined with ascorbic acid (black bars) were incubated with the indicated treatment. Cell culture and statistics are the same as in Fig. 2

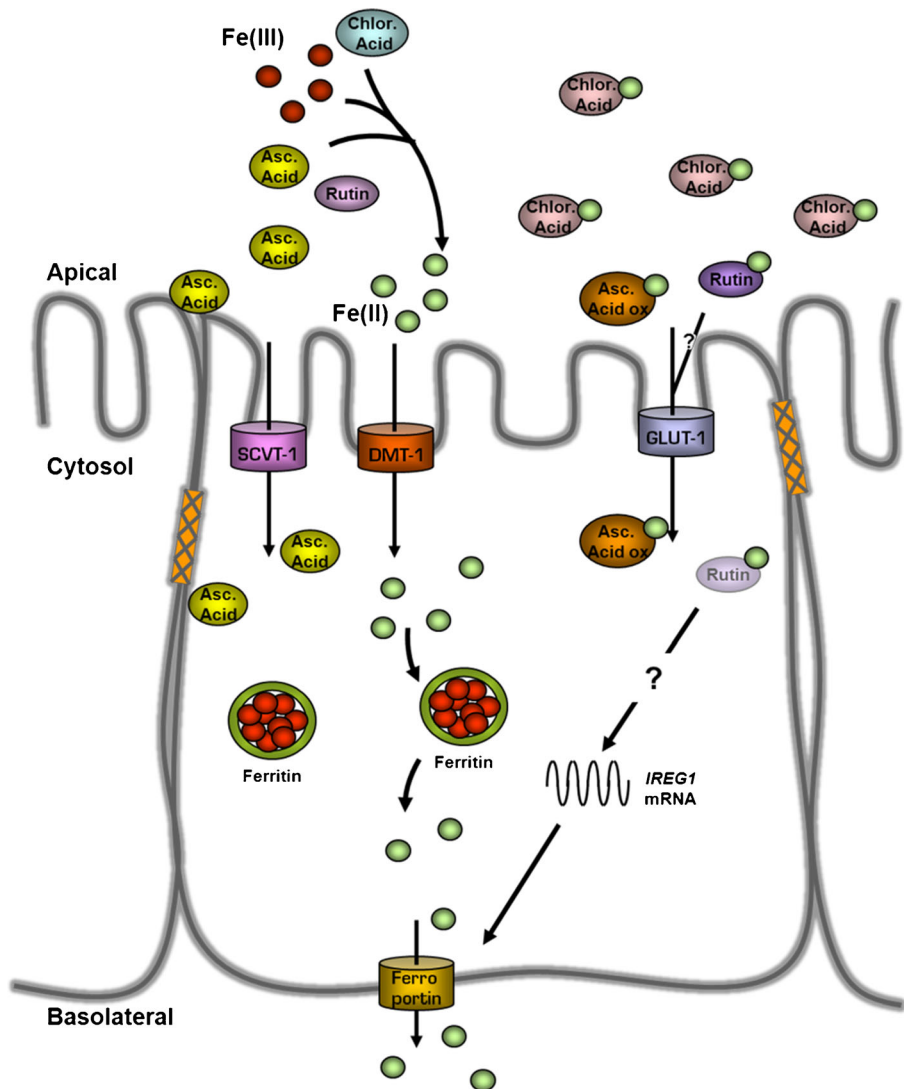


Fig. 4 Suggested mechanism of iron uptake, storage and redistribution induced by ascorbic acid (*Asc. Acid*), chlorogenic acid (*Chlor. Acid*) and rutin in Caco-2 cells. Fe(III) has to be reduced into Fe(II) to be taken in charge by the divalent metal-ion transporter (DMT-1). Ascorbic acid reduces Fe(III) to Fe(II) and induces that way an increased iron uptake. Chlorogenic acid chelates iron at pH 7 and may therefore antagonise iron uptake induced by ascorbic acid. Reduced ascorbic acid is taken up by an ascorbic acid transporter (SVCT-1), but oxidised ascorbic acid may be transported via the glucose transporter GLUT-1. Rutin linked with iron could follow that path or, more likely, exert its activity on ferritin synthesis through the reduction of Fe(III) to Fe(II)

amount of phenolic compound that is absorbed could be responsible for an intracellular effect, as it was recently described for ascorbic acid.

A recent study performed by our group shows that iron uptake, as evaluated by a ferritin assay, into intestinal human cells decreases after incubation with the intestinal phase of *in vitro* digestion, presumably due to the presence of chlorogenic acid and other phenolic compounds (Miranda et al. 2013). Interestingly, a recent study indicates

that the oxidation of phenolic compounds, using a pre-treatment with polyphenol oxidase, could be a promising way to increase the availability of iron in legume food (Luo and Xie 2013).

Impact Of Potato Consumption on Human Health

A review of the available epidemiological studies reveals conflicting results regarding potato consumption and risk of type 2 diabetes and cardiometabolic health (Camire et al 2009; McGill et al. 2013). Potato consumption has been suspected of contributing to type 2 diabetes and obesity mainly because of its high carbohydrate levels, presenting high glycemic index (GI) and processing as French fries (Halton et al. 2006). However, GI values for potato vary greatly due to compositional differences among cultivars (Henry et al. 2005) and methods of food preparation (Fernandes et al. 2005), suggesting that consumer choices may influence this negative impact. Interestingly, when cooking is followed by cooling, amylose retrogrades to produce resistant starch, slowing the post-prandial glucose release and thereby reducing GI (Leeman et al. 2005). Recent studies on potato composition revealed, however, that there is much more in potatoes than starch. Indeed, it contains important phytochemicals that may have a positive impact on human health and prevent the development of type 2 diabetes, cardiovascular diseases and certain types of cancers. In particular, 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 (McGill et al. 2013). The content in dietary fibres and phenolic compound is of particular interest as therapeutic aid for diabetes. Chlorogenic acid appears to increase insulin sensitivity, reduce gut glucose absorption and inhibit gluconeogenesis (Ong et al. 2013). A correlation between polyphenol intake and reduced incidence of cancers, cardiovascular and neurodegenerative diseases has also been shown in several studies, although their positive effects could not only be attributed to their antioxidant properties. The health benefits of polyphenols are now being explained by a multitude of “non-antioxidant” complex activities including anti-inflammatory and other effects that do not involve necessarily a free radical inhibition. According to the recent literature, one can thus hypothesise that several of the potato polyphenols may exert some non-antioxidant beneficial health effects. For instance, it has been reported that chlorogenic acid inhibits the proliferation of human cancer cells through the inhibition of transcription factors (activator protein-1 and NF- κ B) and protein kinases (MAPKs) as well as the induction of phase 2 detoxifying enzyme activity (Feng et al. 2005). Interestingly, the benefits of the consumption of purple-fleshed potatoes on health have been stressed in several animal and human studies. It is worth noting that these purple-fleshed potatoes contained generally, in addition to anthocyanins, higher chlorogenic acid concentrations as compared with their white-fleshed counterparts. The health benefits included improvement of the antioxidant status in serum and liver of cholesterol-fed rat (Han et al. 2007), inhibition of carcinogenesis in rats with induced breast cancer (Thompson et al. 2009), and improvement of antioxidant status, reduction of inflammation and DNA damage in humans (Kaspar et al. 2011).

Conclusion

Potato tubers contain interesting amounts of health-promoting components such as vitamin C, phenolic compounds and iron. However, numerous factors, including genotype, environmental conditions, cooking and processing, may influence their composition. Therefore, it leaves the grower, the manufacturer and/or the consumer with some possibilities to manipulate this composition: choice of variety, optimising soil or stress conditions, optimising storage conditions, developing products and cooking procedures to retain or eliminate certain compounds, etc. The positive or negative effects of potato components on health will finally result from their bioavailability, which depends on the interactions of the various components present within potato or in the consumed meal more generally. Whereas the consumption of a potato cultivar with high level of phenolic compounds may improve the health status of an individual regarding its risk of developing chronic diseases on the one hand, it may dramatically reduce iron absorption on the other one putting an individual at risk of micronutrient deficiency. Therefore, the consumption of a particular potato genotype, submitted to particular “pre-consumption” processes, may not be relevant for all individuals. It stresses the requirement of tailoring potato products to match population nutritional needs. Further controlled intervention trials would, however, be needed to improve our knowledge on the impact of potatoes on health. The various aspects of bioavailability should be, meanwhile, evaluated using a larger and non-targeted metabolomics approach.

References

- Afanas'ev IB, Derozhko AI, Brodskii AV, Kostyuk VA, Potapovitch AI (1989) Chelating and free radical scavenging mechanisms of inhibitory action of rutin and quercetin in lipid peroxidation. *Biochem Pharmacol* 38:1763–1769
- Alvarez-Hernandez X, Smith M, Glass J (1994) Regulation of iron uptake and transport by transferrin in Caco-2 cells, an intestinal cell line. *Biochimica et Biophysica Acta (BBA)-Biomembranes* 1192:215–222
- Anderson KA, Magnuson BA, Tschirgi ML, Smith B (1999) Determining the geographic origin of potatoes with trace metal analysis using statistical and neural network classifiers. *J Agric Food Chem* 47:1568–1575
- Andre CM, Ghislain M, Bertin P, Oufir M, Herrera MDR, Hoffmann L, Hausman J-F, Larondelle Y, Evers D (2007a) Andean potato cultivars (*Solanum tuberosum* L.) as a source of antioxidant and mineral micronutrients. *J Agric Food Chem* 55:366–378
- 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* 55:10839–10849
- Andre CM, Oufir M, Hoffmann L, Hausman J-F, Rogez H, Larondelle Y, Evers D (2009a) Influence of environment and genotype on polyphenol compounds and in vitro antioxidant capacity of native Andean potatoes (*Solanum tuberosum* L.). *J Food Compos Anal* 22:517–524
- Andre CM, Schafleitner R, Guignard C, Oufir M, Aliaga CAA, Nomberto G, Hoffmann L, Hausman J-F, Evers D, Larondelle Y (2009b) 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* 57:599–609
- Ariza-Nieto M, Blair MW, Welch RM, Glahn RP (2007) Screening of iron bioavailability patterns in eight bean (*Phaseolus vulgaris* L.) genotypes using the Caco-2 cell in vitro model. *J Agric Food Chem* 55: 7950–7956
- Barba AA, Calabretti A, d' Amore M, Piccinelli AL, Rastrelli L (2008) Phenolic constituents levels in cv. Agria potato under microwave processing. *Food Sci Technol* 41:1919–1926

- Blessington T, Nzaramba MN, Scheuring DC, Hale AL, Reddivari L, Miller JC Jr (2010) Cooking methods and storage treatments of potato: Effects on carotenoids, antioxidant activity, and phenolics. *Am J Potato Res* 87:479–491
- Bohn T (2014) Dietary factors affecting polyphenol bioavailability. *Nutr Rev* 72:429–452
- Brown C (2008) Breeding for phytonutrient enhancement of potato. *Am J Potato Res* 85:298–307
- Brown CR, Haynes KG, Moore M, Pavek MJ, Hane DC, Love SL, Novy RG, Miller J Jr (2010) Stability and broad-sense heritability of mineral content in potato: Iron. *Am J Potato Res* 87:390–396
- Brune M, Rossander L, Hallberg L (1989) Iron absorption and phenolic compounds: importance of different phenolic structures. *Eur J Clin Nutr* 43:547–557
- Burgos G, Amoros W, Morote M, Stangoulis J, Bonierbale M (2007) Iron and zinc concentration of native Andean potato cultivars from a human nutrition perspective. *J Sci Food Agric* 87:668–675
- Burgos G, Auqui S, Amoros W, Salas E, Bonierbale M (2009a) Ascorbic acid concentration of native Andean potato varieties as affected by environment, cooking and storage. *J Food Compos Anal* 22:533–538
- Burgos G, De Haan S, Salas E, Bonierbale M (2009b) Protein, iron, zinc and calcium concentrations of potatoes following traditional processing as “chuño”. *J Food Compos Anal* 22:617–619
- Burgos G, Salas E, Amoros W, Auqui M, Muñoz L, Kimura M, Bonierbale M (2009c) Total and individual carotenoid profiles in *Solanum phureja* of cultivated potatoes: I Concentrations and relationships as determined by spectrophotometry and HPLC. *J Food Compos Anal* 22:503–508
- Burgos G, Muñoz L, Sosa P, Bonierbale M, zum Felde T, Diaz C (2013) In vitro bioaccessibility of lutein and zeaxanthin of yellow fleshed boiled potatoes. *Plant Foods Hum Nutr* 68:385–390
- Burlingame B, Mouillé B, Charrondière R (2009) Nutrients, bioactive non-nutrients and anti-nutrients in potatoes. *J Food Compos Anal* 22:494–502
- Camire ME, Kubow S, Donnelly DJ (2009) Potatoes and human health. *Crit Rev Food Sci Nutr* 49:823–840
- Chantrét I, Rodolosse A, Barbat A, Dussaulx E, Brot-Laroche E, Zweibaum A, Rousset M (1994) Differential expression of sucrase-isomaltase in clones isolated from early and late passages of the cell line Caco-2: evidence for glucose-dependent negative regulation. *J Cell Sci* 107:213–225
- Chatterjee C, Gopal R, Dube B (2006) Impact of iron stress on biomass, yield, metabolism and quality of potato (*Solanum tuberosum* L.). *Sci Hortic* 108:1–6
- Clifford MN (2004) Diet-derived phenols in plasma and tissues and their implications for health. *Planta Med* 70:1103–1114
- Coleman WK (2000) Physiological ageing of potato tubers: A Review. *Ann Appl Biol* 137:189–199
- Dale MFB, Griffiths DW, Todd DT (2003) Effects of genotype, environment, and postharvest storage on the total ascorbate content of potato (*Solanum tuberosum*) tubers. *J Agric Food Chem* 51:244–248
- Deußer H, Guignard C, Hoffmann L, Evers D (2012) Polyphenol and glycoalkaloid contents in potato cultivars grown in Luxembourg. *Food Chem* 135:2814–2824
- Dixon RA, Paiva NL (1995) Stress-induced phenylpropanoid metabolism. *Plant Cell* 7:1085–1097
- Ezekiel R, Singh N, Sharma S, Kaur A (2013) Beneficial phytochemicals in potato — a review. *Food Res Int* 50:487–496
- FAO (2014) FAOSTAT data: <http://faostat.fao.org>. Accessed 12 Oct 2014
- Feng R, Lu Y, Bowman LL, Qian Y, Castranova V, Ding M (2005) Inhibition of activator protein-1, NF- κ B, and MAPKs and induction of phase 2 detoxifying enzyme activity by chlorogenic acid. *J Biol Chem* 280: 27888–27895
- Fernandes G, Velangi A, Wolever T (2005) Glycemic index of potatoes commonly consumed in North America. *J Am Diet Assoc* 105:557–562
- 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* 141:2864–2872
- Glahn RP, Lee OA, Yeung A, Goldman MI, Miller DD (1998) Caco-2 cell ferritin formation predicts nonradiolabeled food iron availability in an in vitro digestion/Caco-2 cell culture model. *J Nutr* 128: 1555–1561
- Gunshin H, Mackenzie B, Berger UV, Gunshin Y, Romero MF, Boron WF, Nussberger S, Gollan JL, Hediger MA (1997) Cloning and characterization of a mammalian proton-coupled metal-ion transporter. *Nature* 388:482–488
- Halton TL, Willett WC, Liu S, Manson JE, Stampfer MJ, Hu FB (2006) Potato and french fry consumption and risk of type 2 diabetes in women. *Am J Clin Nutr* 83:284–290
- Hamouz K, Lachman J, Pazder K, Hejtmánková K, Cimr J, Musilová J, Pivec V, Orsák M, Svobodová A (2013) Effect of cultivar, location and method of cultivation on the content of chlorogenic acid in potatoes with different flesh colour. *Plant Soil Environ* 59:465–471

- Han KH, Matsumoto A, Shimada K, Sekikawa M, Fukushima M (2007) Effects of anthocyanin-rich purple potato flakes on antioxidant status in F344 rats fed a cholesterol-rich diet. *Br J Nutr* 98: 914–921
- Haynes K, Yencho G, Clough M, Henninger M, Sterrett S (2012) Genetic variation for potato tuber micronutrient content and implications for biofortification of potatoes to reduce micronutrient malnutrition. *Am J Potato Res* 89:192–198
- Henry CJK, Lightowler HJ, Strik CM, Storey M (2005) Glycaemic index values for commercially available potatoes in Great Britain. *Br J Nutr* 94:917–921
- Hurrell RF, Reddy M, Cook JD (1999) Inhibition of non-haem iron absorption in man by polyphenolic-containing beverages. *Br J Nutr* 81:289–295
- Hynes MJ, O’Coineann M (2004) The kinetics and mechanisms of reactions of iron (III) with caffeic acid, chlorogenic acid, sinapic acid, ferulic acid and naringin. *J Inorg Biochem* 98:1457–1464
- Kalt W (2005) Effects of production and processing factors on major fruit and vegetable antioxidants. *J Food Sci* 70:R11–R19
- 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* 141:108–111
- Lane DJ, Richardson DR (2014) The active role of vitamin C in mammalian iron metabolism: Much more than just enhanced iron absorption! *Free Radic Biol Med* 75:69–83
- Lawen A, Lane DJ (2013) Mammalian iron homeostasis in health and disease: uptake, storage, transport, and molecular mechanisms of action. *Antioxid Redox Signal* 18:2473–2507
- Leeman M, Östman E, Björck I (2005) Vinegar dressing and cold storage of potatoes lowers postprandial glycaemic and insulinaemic responses in healthy subjects. *Eur J Clin Nutr* 59:1266–1271
- Lefèvre I, Ziebel J, Guignard C, Hausman J-F, Gutiérrez Rosales RO, Bonierbale M, Hoffmann L, Schafleitner R, Evers D (2012) Drought impacts mineral contents in Andean potato cultivars. *J Agron Crop Sci* 198: 196–206
- Lewis CE, Walker JR, 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
- Love S, Pavsek J (2008) Positioning the potato as a primary food source of vitamin C. *Am J Potato Res* 85: 277–285
- Luo Y-W, Xie W-H (2013) Effects of polyphenol oxidation on in vitro iron availability in faba bean (*Vicia faba* L.) flour. *Int J Food Sci Technol* 48:701–706
- McCullough ML, Peterson JJ, Patel R, Jacques PF, Shah R, Dwyer JT (2012) Flavonoid intake and cardiovascular disease mortality in a prospective cohort of US adults. *Am J Clin Nutr* 95:454–464
- McGill CR, Kurilich AC, Davignon J (2013) The role of potatoes and potato components in cardiometabolic health: A review. *Ann Med* 45:467–473
- Miller PE, Snyder DC (2012) Phytochemicals and cancer risk: a review of the epidemiological evidence. *Nutr Clin Pract* 27:599–612
- 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* 4:1595–1601
- Ong KW, Hsu A, Tan BKH (2013) Anti-diabetic and anti-lipidemic effects of chlorogenic acid are mediated by ampk activation. *Biochem Pharmacol* 85:1341–1351
- Paget M, Amoros W, Salas E, Eyzaguirre R, Alspach P, Apiolaza L, Noble A, Bonierbale M (2014) Genetic evaluation of micronutrient traits in diploid potato from a base population of Andean Landrace Cultivars. *Crop Sci* 54:1949–1959
- Peñarrieta JM, Salluca T, Tejeda L, Alvarado JA, Bergenstahl B (2011) Changes in phenolic antioxidants during chuño production (traditional Andean freeze and sun-dried potato). *J Food Compos Anal* 24:580–587
- Reyes L, Miller J, Cisneros-Zevallos L (2004) Environmental conditions influence the content and yield of anthocyanins and total phenolics in purple-and red-flesh potatoes during tuber development. *Am J Potato Res* 81:187–193
- Rosenthal S, Jansky S (2008) Effect of production site and storage on antioxidant levels in specialty potato (*Solanum tuberosum* L.) tubers. *J Sci Food Agric* 88:2087–2092
- Søltøft M, Nielsen J, Holst Laursen K, Husted S, Halekoh U, Knuthsen P (2010) Effects of organic and conventional growth systems on the content of flavonoids in onions and phenolic acids in carrots and potatoes. *J Agric Food Chem* 58:10323–10329
- Stevenson DE, Hurst RD (2007) Polyphenolic phytochemicals-just antioxidants or much more? *Cell Mol Life Sci* 64:2900–2916

- Tako E, Beebe SE, Reed S, Hart JJ, Glahn RP (2014) Polyphenolic compounds appear to limit the nutritional benefit of biofortified higher iron black bean (*Phaseolus vulgaris* L.). *Nutr J* 13:28
- Thompson B (2007) Food-based approaches for combating iron deficiency. In *Nutritional Anemia* p 337–358. Sight and Life Press, Basel, Switzerland
- Thompson MD, Thompson HJ, McGinley JN, Neil ES, Rush DK, Holm DG, Stushnoff C (2009) Functional food characteristics of potato cultivars (*Solanum tuberosum* L.): Phytochemical composition and inhibition of 1-methyl-1-nitrosourea induced breast cancer in rats. *J Food Compos Anal* 22:571–576
- Vlachodimitropoulou E, Sharp PA, Naftalin RJ (2011) Quercetin–iron chelates are transported via glucose transporters. *Free Radic Biol Med* 50:934–944
- White PJ, Broadley MR (2005) Biofortifying crops with essential mineral elements. *Trends Plant Sci* 10:586–593
- WHO/FAO (2002) Joint WHO/FAO Expert Consultation on Diet, Nutrition and the Prevention of Chronic Diseases. WHO technical report series, Geneva, Switzerland
- Woolfe JA, Poats SV (1987) The potato in the human diet. Cambridge University Press, Cambridge
- Zou Y, Lu Y, Wei D (2004) Antioxidant activity of a flavonoid-rich extract of *Hypericum perforatum* L. in vitro. *J Agric Food Chem* 52:5032–5039