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Developing the Nutritional Potential of Potato

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ABSTRACT

Potatoes are the most consumed vegetable in the developed world and consumption is increasing in the developing world. Consequently, the phytonutrient content of potato can have a large impact on public health. Moreover, because of the high consumption even modest increases in tuber phytonutrient content can be important. Although already a good source of phytonutrients, little effort has been directed towards maximizing the nutritional potential of potatoes. Similarly, the rich genetic diversity of potatoes has barely been utilized for nutritional enhancement. Recent technological advances combined with increasing knowledge about which phytochemicals have health-promoting properties should facilitate the development of phytonutrient-enhanced potatoes. This review will focus on phenolic, glycoalkaloid, vitamin C and vitamin B_9 (folate) content in potato and examine recent efforts to further increase tuber concentrations of these compounds.

Keywords: folate, flavonols, glycoalkaloids phytonutrients, phenolics

Abbreviations: CGA, chlorogenic acid; **GA**, glycoalkaloids; **LCMS**, liquid chromatography; **QTL**, quantitative trait loci; **RDA**, recommended daily allowance; mass spectrometry

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INTRODUCTION

As the most consumed vegetable in the West, potato has considerable potential to be an even more important source of valuable dietary vitamins, phytonutrients and minerals (Tudela *et al.* 2002; Lin 2004). Because of its high consumption, potato has more dietary relevance and impact than foods eaten in sparse quantities. Furthermore, in the developing world potato consumption is increasing at roughly 5% a year. In 2005 the developing world for the first time produced more potatoes than the developed world, with China and India producing about 1/3rd of the world's potatoes.

Tubers contain around 80% water and 20% solids, although this varies depending on the cultivar. Of the 20 g of solids in a 100 g tuber, about 18 g is carbohydrate and 2 g protein, primarily patatins that can account for 40% of the soluble protein content (Prat 1990). Potatoes are an important source of many vitamins and minerals. A comparison of the percentage of the recommended daily allowance (RDA) of calories in a given portion size versus the percentage of the RDA of vitamins and minerals in that same portion, shows the intake of many vitamins and minerals exceed the percentage of calories. For example, 100 g (3.5 ounces) of potatoes contains 4% of the RDA calorie intake, 33% of the RDA of Vitamin C, and 12% of RDA for potassium.

Opportunities for nutritional enhancement

For efforts to further enhance the nutritional value of potatoes, researchers are fortunate that potatoes may contain more genetic diversity than any other crop. This diversity may reflect the ability of potatoes to grow in remarkably divergent environments, from arid alpine highlands to tropical rainforests to just below the Arctic Circle and even on tree branches (Hawkes 1990). This genetic diversity has barely been tapped into for nutritional enhancement, as modern cultivars are estimated to contain less than 1% of the available genetic diversity of wild species. About 200 wild potato species exist, along with thousands of primitive varieties (Spooner *et al.* 2005).

Historically, little effort has been directed towards improving the nutritional value of any crop. Potatoes were domesticated between 7000-10000 years ago, likely around Lake Titicaca, an alpine lake at 12,500 feet in the Andes between Peru and Bolivia (Spooner *et al.* 2005), and development of potatoes in the pre-modern, pre-scientific era likely selected for varieties with improved traits such as yield, taste, appearance, size and disease resistance. Even

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modern potato breeding programs focus on developing cultivars with such traits, with little attention paid to increasing phytonutrient content, perhaps because these other traits have been considered more important, along with the technical difficulty of enhancing phytonutrients.

However, the opportunities to improve a crop's nutritional value have been markedly increased by recent scientific developments. Perhaps the three most important technological advances for nutritional enhancement are the molecular biology toolkit, improved instrumentation and medical advances. Molecular biological approaches have allowed the pathways of many vitamins and phytonutrients to be elucidated, identified key genes and enabled transgenic, marker-assisted selection, and mapping strategies.

Improved and more affordable LCMS and GCMS instrumentation facilitates nutritional enhancement. Metabolome analysis is a powerful, still maturing technology that has been used with great effect in plant research. An analysis of 14 *Arabidopsis* accessions using LC-QTOF MS detected over 2000 mass signals of which only 13% were present in all the accessions. Furthermore, the researchers were able to assign QTLs for 75% of the mass peaks (Keurentjes *et al.* 2006). Metabolic profiling was used to characterize phytonutrients in tomato fruit (Moco *et al.* 2006; Schauer *et al.* 2006; Fraser *et al.* 2007). MS profiling in potato has been used to show substantial equivalence between transgenic 'Desiree' and the wild type (Roessner *et al.* 2001; Catchpole *et al.* 2005). For the compositional analysis of potato tubers, FIE-MS was used to assess compounds affecting traits including flavor and aroma (Beckmann *et al.* 2007).

Although medical studies are increasingly clarifying which phytonutrients have health-promoting effects, the lack of this type of information is probably the biggest bottleneck in developing more nutritious crops. Much more information is needed about thousands of individual phytochemicals. Especially needed is information about

- the full extent of the health-promoting characteristics for a given phytochemical
- possible synergistic effects with other phytochemicals
- the bioavailability of the compound
- whether the amounts present in a food are sufficient to be physiologically relevant
- whether increasing the amount of a phytochemical would provide additional health benefits.

Vitamin C

Potatoes are a well-known source of Vitamin C, with a medium red potato (173 g) providing 36% of the RDA according to the USDA databases. Vitamin C (**Fig. 1**) detoxifies reactive oxygen species in plants, which are the primary source of vitamin C in the human diet. Leafs and chloroplasts can contain 5 to 25 mM L-ascorbate respectively (Wheeler *et al.* 1998). Plants may have multiple vitamin C biosynthetic pathways and all of the enzymes of the L-galactose pathway have been recently characterized (Laing *et al.* 2007; Wolucka and Montagu 2007).

Ascorbate in cultivated potatoes ranges from about 11 to 40 mg/100 g FW (Love and Pavek 2008). One study of Vitamin C content in 75 genotypes found concentrations ranging from 11.5 to 29.8 mg/100 g FW (Love *et al.* 2004). This study also reported that some genotypes had more consistent concentrations of vitamin C than others across multiple years or when grown in different locations and suggested that the year may have a bigger effect than location. Another study measured vitamin C in 33 cultivars grown in 3 locations around Europe (Dale *et al.* 2003). If these results in dry weight are converted to fresh weight assuming potatoes are 80% water, a range of 13-30.8 mg vitamin C per 100 g FW is obtained. The heritability of ascorbate content is high, suggesting levels can be increased through traditional breeding approaches (Love and Pavek 2008).

Vitamin C levels decrease rapidly as much as 60% during cold storage of potatoes, (Keijbets and Ebbenhorst-Seller 1990). After placing 33 genotypes in cold storage for 15-17 weeks, large decreases in vitamin C were observed compared to pre-storage, ranging from 20-60% depending on the genotype (Dale *et al.* 2003). These authors make the important point that breeding efforts to increase vitamin C should focus on post-storage content and that in most cases this is more relevant than fresh-harvest concentrations. This will less applicable for developing countries that make limited use of cold storage and for which post-harvest loses consequently should be less.

A study examining the effect of freeze-storing peeled, blanched then fried potatoes, found a 10% loss of vitamin C after 6 months of storage at -18°C (Tosun and Yücecan 2008). However, a 51% loss occurred during pre-freezing treatment, which sounds a cautionary note about the importance of how potatoes are handled during processing. Some of our studies with skin-on potatoes cooked using microwaving, frying, steaming, baking or boiling, showed a negligible loss of vitamin C (Navarre, unpublished results). In the absence of cultivars with stable vitamin C levels during cold storage, one solution to minimize post-harvest loss would be minimally destructive cooking of tubers shortly after harvest, followed by flash-freezing of the product.

Wounding can increase vitamin C levels. Potatoes stored for 2 days following slicing or bruising had a 400% increase in vitamin C in sliced tubers, but a 347% decrease in bruised tubers (Mondy and Leja 1986). Vitamin C levels in fresh-cut potatoes stored in air increased, whereas levels decreased in those stored frozen or in a modified atmosphere (Tudela *et al.* 2002b). Such results suggest that wounding of potatoes can be used to increase vitamin C in commercial products; however, before such a strategy to increase vitamin C is adopted, a method must be found to decrease the browning that can occur in cut tissue.

Folate

Potato is a significant source of dietary folate (vitamin B_9) because of its high consumption. There are several forms of folates, but in potato the most abundant form is 5-methyltetrahydrofolate (**Fig. 1**), which comprised over 90% of the total tuber folate (Konings *et al.* 2001). Several studies show potatoes are a leading source of dietary folate in Europe. In the Netherlands, potatoes were the most important source of dietary folate among vegetables, supplying 10% of the intake (Brussaard *et al.* 1997). A separate study reported that potatoes were the third most important source in the Dutch diet, providing 7% of the total folate intake (Konings *et al.* 2001). Potatoes provided 9–12% of the total folate intake in a Norwegian study (Brevik *et al.* 2005) and ~10% of the Finnish intake (Vahteristo *et al.* 1997; Alfthan *et al.* 2003).

Folate concentrations in raw potatoes vary between 12 and 37 µg/100 g FW (Holland *et al.* 1996; Vahteristo *et al.* 1997; Konings *et al.* 2001). The USDA Database (SR20) gives values of 14 and 18 µg/100 g FW for raw potatoes. We determined total folate concentrations in potato tubers from over 70 cultivars, breeding lines, and wild species and found values ranging from 0.46 to 1.37 µg/g DW (Goyer and Navarre 2007). Seven of the top ten varieties were yellow fleshed, but yellow color was not always associated with high folate concentrations. 'Winema' and 'Ranger Russet' had the highest amounts of folate among white-fleshed cultivars (0.95 and 1.04 µg/g DW, respectively). Among the top yellow cultivars were 'Golden Sunburst,' 'Satina,' and 'Carola.' *Solanum pinnatisectum* had the highest folate concentrations among wild species and the highest folate content of all genotypes analyzed on a fresh weight basis (0.35 µg/g FW). Despite the small number of wild species analyzed, a ~2-fold difference was found between the lowest and the highest genotypes among those species, suggesting that wild species are good candidates for additional screening.

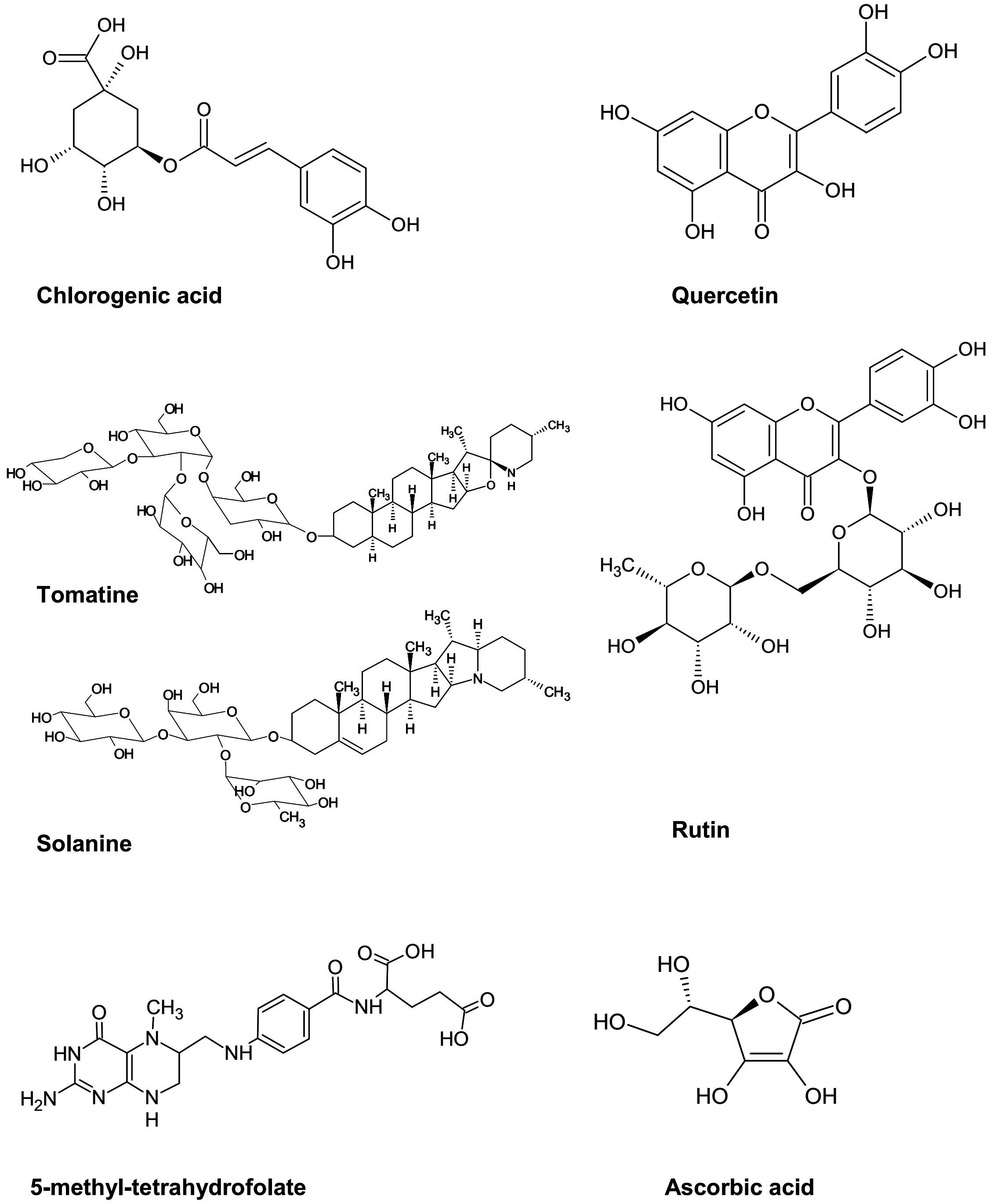

Fig. 1 The structure of various potato phytochemicals.

Effect of cooking on folate

One study showed boiling potatoes for 60 minutes resulted in a less than 20% decrease in folate content whether or not skin was retained (McKillop *et al.* 2002). Folate concentrations for cooked French fries, boiled potatoes and fried potatoes were similar to those in raw potatoes (Konings *et al.* 2001). However, a different study found a 35 and 52% decrease in fries and boiled potatoes compared to raw potatoes (Vahteristo *et al.* 1997). A study of the effect of four cooking methods on folate concentration found that the overall retention of folate was greater than 70% (Augustin *et al.* 1978). Boiled, peeled samples had lower folate concentrations than unpeeled samples. In addition to its positive effect on folate retention, skin has higher folate concentrations than flesh (Augustin *et al.* 1999; Goyer and Navarre 2007).

Increasing folate content in potatoes

No attempt has been made to increase folate in potatoes through breeding. We showed a ~3-fold difference in folate values amongst >70 potato genotypes (Goyer and Navarre 2007). A ~7.5-fold difference in folate was reported among nine strawberry genotypes (Tulipani *et al.* 2008), whereas smaller variations were reported for pulses and rye (Kariluoto *et al.* 2001; Han and Tyler 2003), but only a few genotypes were analyzed in each case. Crossing high-folate potato genotypes could be an effective strategy.

The folate biosynthetic pathway in plants has recently been characterized, allowing the enhancement of folate levels in tomato and rice by overexpressing the first enzyme of both the para-aminobenzoic acid and the pteridine branches of the folate pathway (Diaz de la Garza *et al.* 2007; Storozhenko *et al.* 2007). We used a similar strategy in potatoes, expressing the genes under a tuber-specific promoter and preliminary results suggest a greater than 6-fold increase occurred in tuber folate concentrations (Goyer and

Navarre, unpublished results). Additional strategies for folate metabolic engineering have been described in recent reviews (Basset *et al.* 2005; Rébeillé *et al.* 2006; Bekaert *et al.* 2008) and include increasing the proportion of 5-formyl-THF, sequestering folates into vacuoles, increasing folate salvage capacity and over-expressing the folate-binding protein. A folate biofortified potato could be an important tool to combat global folate deficiency.

Glycoalkaloids

Potatoes contain glycoalkaloids (GAs), which are steroidal alkaloids comprised of a heterocyclic nitrogen, and a C_{27} steroid conjugated to a sugar moiety, most commonly a tri- or tetrasaccharide. GAs are secondary metabolites and their role in plants is to contribute to pest and pathogen resistance. From a dietary standpoint, GAs are undesirable because they can cause vomiting and other ill effects if ingested in high enough amounts (McMillan and Thompson 1979; Hopkins 1995). Furthermore, GAs can cause a bitter taste at high concentrations (Sinden *et al.* 1976). Newly developed potato varieties in the United States must contain less than 20 mg/100 g FW of total GAs (Wilson 1959) but the guidelines established in other countries varies.

Recent evidence complicates assessment of the desirability of GAs in the diet because GAs can also have health-promoting effects, such as inhibition of mice tumors by a solamarine (Kupchan *et al.* 1965) and protection against skin cancer (Cham 1994). GAs including tomatine, solanine and chaconine were shown to inhibit growth of human colon and liver cancer cells in cell culture assays (Lee *et al.* 2004; Friedman *et al.* 2005) with a potency similar to the anticancer drug adriamycin. Anticancer effects were observed in assays using cervical, lymphoma and stomach cancer cells and treatments using two or more GAs suggested both synergistic and additive effects (Friedman *et al.* 2005). Dietary tomatine was effective against cancer in a feeding study using rainbow trout (Friedman *et al.* 2007). Tomatidine can act as a chemosensitizing agent, increasing the effectiveness of cancer chemotherapy by inhibiting multidrug resistance in human cancer cells (Lavie *et al.* 2001). Chaconine was shown to reduce metastasis and it was suggested this may allow new chemotherapeutic approaches (Shih *et al.* 2007). A separate study showed that solamargine, a glycoalkaloid found in some potatoes, increased the susceptibility of two different types of human lung cancer cell lines to several anticancer drugs (Liang *et al.* 2008).

Beyond chemopreventitive effects, GAs were shown to boost the immune response in mice fed GAs that were more resistance to infection by Salmonella (Gubarev *et al.* 1998). Tomatine was demonstrated to potentiate the mice immune response to vaccines (Rajananthanan *et al.* 1999). GAs are reported to inactivate several types of herpes viruses (Chataing *et al.* 1997).

Thus a more nuanced approached to tuber GA content may be in order that more carefully considers the possible effects of individual GAs, of which potatoes have many different types.

Potato GA diversity

Most potato GAs are solanidanes such as solanine (**Fig. 1**) or spirosolanes, such as tomatine (**Fig. 1**). Solanine and chaconine, often comprise upwards of 90% of the total GA complement of domesticated potatoes (Griffiths *et al.* 1997; Sotelo and Serrano 2000), but estimates have been made that the potato family contains about 90 GAs (Friedman and McDonald 1997). Using LCMS analysis, we found that GAs are a major source of small molecule diversity in tubers. In our study of tubers from four wild potato species and three cultivars, about 100 GAs were tentatively identified (Shakya and Navarre 2008; unpublished results) that were a roughly equal mix of solanidanes and spirosolanes. The occurrence of this number of GAs was unexpected given only seven genotypes were analyzed. Moreover, these GAs were found in tubers, which are known to have much lower GA concentrations than leaves, sprouts, flowers or leaves.

Thus, potatoes may have a much greater diversity of GAs than previously realized, which may offer opportunities for the production of future cultivars with a more optimal GA compliment. The predominance of solanine and chaconine in modern Western cultivars may be due to the fact that only a tiny percentage of available potato germplasm was used in the breeding of these cultivars and reflects something of a bottleneck in the genetic diversity of commercial cultivars.

Before it will be possible to develop potatoes with an ideal GA complement, much more medical information about the bioavailability, dietary significance and both positive and negative effects on health of individual GAs is needed. It is expected that some GAs will have much lower toxicity than others and differing health-promoting efficacy.

Tuber phenolic compounds: phenolic acids, flavonols and anthocyanins

Potatoes are an important source of dietary phenolics, the most abundant antioxidants in the diet. Phenolics have additional health-promoting effects including on longevity, mental acuity and eye health (Parr and Bolwell 2000; Manach *et al.* 2004; Scalbert *et al.* 2005). Upon consumption, phenolics are metabolized and have a wide range of bioavailability not yet thoroughly defined (Manach *et al.* 2004). A study of 74 Andean potato landraces found an ~11-fold variation in total phenolics and a high correlation between phenolics and total antioxidant capacity (Andre *et al.* 2007). We screened tubers from hundreds of cultivars and wild potato species for phenolics and found over a 15-fold difference in the amount of phenolics in different potato genotypes (Navarre and Shakya, unpublished data). White-fleshed cultivars are preferred in many countries and can contain generous amounts of phenolics, many of which are colorless. 'Russet Norkotah' had high amounts among the white fleshed cultivars at ~4 mg/g DW. A purple-fleshed wild species, *S. pinnatisectum*, had over 5 mg/g DW total phenolics. Among the numerous genotypes we screened, purple-fleshed lines had the highest amounts of phenolics, with several genotypes containing over 10 mg/g DW total phenolics.

A comparison of high-phenolic potatoes to some published reports of total phenolic amounts found in other vegetables show these potatoes have more phenolics than tomatoes, peas, onions, French beans, white cabbage, carrots, lettuce, or cucumbers (Navarre, unpublished results). Moreover, the amounts in high-phenolic potatoes approximate reported phenolic amounts for broccoli, Brussels sprouts and spinach. Thus, potatoes can be a substantial source of phenolics in the diet and compare favorably to other vegetables. An evaluation of the contribution of 34 fruits and vegetables to phenolic intake in the American diet concluded that potatoes were the third most important source after apples and oranges (Chun *et al.* 2005). This is despite the fact that the potatoes used in this study were an unspecified variety bought at a supermarket and almost certainly contained a small amount of phenolics relative to high-phenolic potatoes. This highlights the potential to further increase the nutritional value of potato by more fully utilizing and marketing existing germplasm.

Tubers actively synthesize numerous phenolic compounds, including phenolic acids, flavonols and anthocyanins (**Fig. 1**). The biosynthetic pathways of many tuber phenolics are known, including for chlorogenic acid (Niggeweg *et al.* 2004), which is the most abundant phenolic in tubers and can comprise over 90% of a tuber's total phenolics (Malmberg and Theander 1985).

Chlorogenic acid has numerous health-promoting effects and anti-viral and anti-bacterial properties. CGA may decrease the risk of type two diabetes (Legrand and Scheen 2007) and slow the release of glucose into the bloodstream

(Bassoli *et al.* 2008), which could be important for lowering the glycemic index value of potatoes. Dietary CGA is bioavailable in humans (Monteiro *et al.* 2007), may reduce the risk of some cancers and heart disease (Nogueira and do Lago 2007) and is also anti-hypertensive (Yamaguchi *et al.* 2007). CGA protects animals against degenerative, age-related diseases when added to their diet.

A concern about high-phenolic potatoes is whether they would have unacceptable levels of browning or after cooking darkening. More recent research has shown that neither the amount of total phenolics, chlorogenic acid or polyphenol oxidase correlate with the amount of browning observed in fresh-cut potatoes and that these compounds were not rate-limiting in the development of browning (Cantos *et al.* 2002). Similarly, a QTL approach found no correlation between browning and chlorogenic acid (Werij *et al.* 2007). Thus concerns that high phenolic levels will absolutely lead to browning problems appear unfounded.

Tuber flavonols

Although tubers contain flavonols such as rutin and quercetin (**Fig. 1**), potatoes have not been considered an important dietary source of flavonols. However, several strategies can be used to increase tuber flavonols. Flavonols increased in fresh-cut tubers, which contained concentrations up to 14 mg/100 g FW of flavonols, and they can be a valuable dietary source at these concentrations because of high consumption (Tudela *et al.* 2002a). Flavonol content in diverse potato germplasm has been little studied. We found over a 30-fold difference in flavonol content among cultivars and wild species (Shakya and Navarre, unpublished results). Recombinant approaches have recently been adopted to boost flavonol levels. We used RNAi to silence hydroxycinnamoyl CoA quinate transferase (HQT) and found a substantial increase in flavonols in tubers, along with a reduction in CGA (Shakya and Navarre, unpublished data). Silencing HQT in tomatoes resulted in an increase in rutin (Cle *et al.* 2008). Overexpressing a MYB transcription factor in tubers resulted in an increase in CGA and a 100-fold increase in kaempferol-rutinose to 0.12 mg/g DW (Rommens *et al.* 2008). Quercetin and related flavonols have multiple health-promoting effects, including reduced risk of heart disease, lowered risk of asthma, bronchitis, and emphysema and reduced risk of some cancers including prostate and lung cancer.

Potatoes, especially colored-fleshed cultivars, can contain substantial amounts of anthocyanins, compounds that can function as antioxidants and have other health-promoting effects. A gene encoding dihydroflavonol 4-reductase is required for production of pelargonidins anthocyanins in potato and other anthocyanin candidate genes have been identified (De Jong *et al.* 2003, 2004). An anthocyanin-enriched fraction from potatoes was found to have anti-cancer properties (Reddivari *et al.* 2007). A screen of 26 colored-fleshed lines for anthocyanin content found up to 7 mg/g FW in the skin and 2 mg/g FW in the flesh (Lewis *et al.* 1998). An evaluation of 31 colored genotypes found a range of 0.5 to 3 mg/g FW in the skin and up to 1 mg/g FW in the flesh (Jansen and Flamme 2006). Another study described whole tubers that contained up to 4 mg/g FW and these anthocyanin concentrations correlated with antioxidant value (Brown *et al.* 2005).

CONCLUDING REMARKS

Potatoes have a complex chemical makeup that belies the mischaracterization by some that they are mostly starch and provide "empty calories." Given that efforts to increase vitamins, phytonutrients and minerals in potatoes are in their infancy, it seems likely that potatoes with even higher amounts of phytonutrients will be developed in the near future. Such potatoes would be growable in diverse geographic regions worldwide and positively impact global health.

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