Maximizing the Nutritional Potential of Potato: the Case of Folate

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Abstract Micronutrient malnutrition, also known as the hidden hunger, affects over two billion people worldwide. Potato is the third most consumed food crop in the world, and is therefore a fundamental element of food security for millions of people. Increasing the amount of micronutrients in potatoes could help alleviate worldwide micronutrient malnutrition. Folate (or vitamin B_9) is an essential micronutrient in the human diet. Deficiencies in folate lead to serious, sometimes lethal, diseases. Unfortunately, folate intake remains suboptimal in both developing and developed regions of the world. This paper uses folate to illustrate various approaches that could be implemented to increase micronutrient content in potato. It provides a brief overview of recent analyses of folate content in diverse potato germplasm, of changes in folate content during tuber development, and of the effect of postharvest low temperature storage of potato on folate content, and how an optimization of these different factors could lead to significant increases in folate intake from potato.

Keyword Hidden hunger, Micronutrients, Vitamins, Biodiversity

Introduction

Micronutrient malnutrition, also known as the hidden hunger, affects over two billion people worldwide (Bouis 2002; Protection 1997). Folate, also known as vitamin B_9, is an essential micronutrient in the human diet. Folate deficiencies have been linked to many serious health concerns such as congenital birth defects, anemia, increased risk of stroke, certain types of cardiovascular diseases and cancers (Bailey et al. 2003; Bazzano et al. 2002; Beaudin and Stover 2007; Voutilainen et al. 2001). Neural tube defects (NTDs) such as spina bifida and anencephaly are some of the most common congenital birth defects, with an estimated 250,000 cases of NTDs worldwide (Youngblood et al. 2013). It is estimated that up to 70% of NTDs can be prevented with proper folate intake or folate supplementation (Beaudin and Stover 2007). Unfortunately, folate intake remains sub-optimal even in countries that have implemented folic acid food fortification (Bentley et al. 2006).

Potato (*Solanum tuberosum* L.) is one of the most consumed food crops worldwide, with a total world production of over 382 million tons in 2014 (FAOSTAT data). It is estimated that over one billion people worldwide consume potatoes regularly (CIP 2015) making this crop a fundamental element of food security for millions of people. For these reasons, the potato is an ideal target for biofortification efforts.

This paper summarizes results of systematic phenotyping of tuber folate content in various potato germplasm, and the effect of tuber development and postharvest low temperature storage on folate content. It also provides a brief snapshot of our research effort to identify genes or markers of folate content that would facilitate folate phenotyping.

Natural Genetic Diversity

Early screening of 61 varieties or advanced breeding lines for folate content using a tri-enzyme extraction and microbial assay showed concentrations varying from 521 to 1,373 ng g^{-1} dry weight (Goyer and Navarre 2007) (Fig.1). Varieties commonly grown in the United States such as Russet Burbank and Ranger Russet had folate concentrations around 1,000 ng g^{-1} dry weight, and the majority of varieties or advanced breeding lines had folate concentrations between 750 and 1,000 ng g^{-1} dry weight. These results indicated that extending folate content phenotyping amongst modern potato germplasm might not be fruitful in identifying high folate content material (i.e. material with folate concentrations above 2,000 ng g^{-1} dry weight, roughly double the content found in most currently consumed potatoes in the United States).

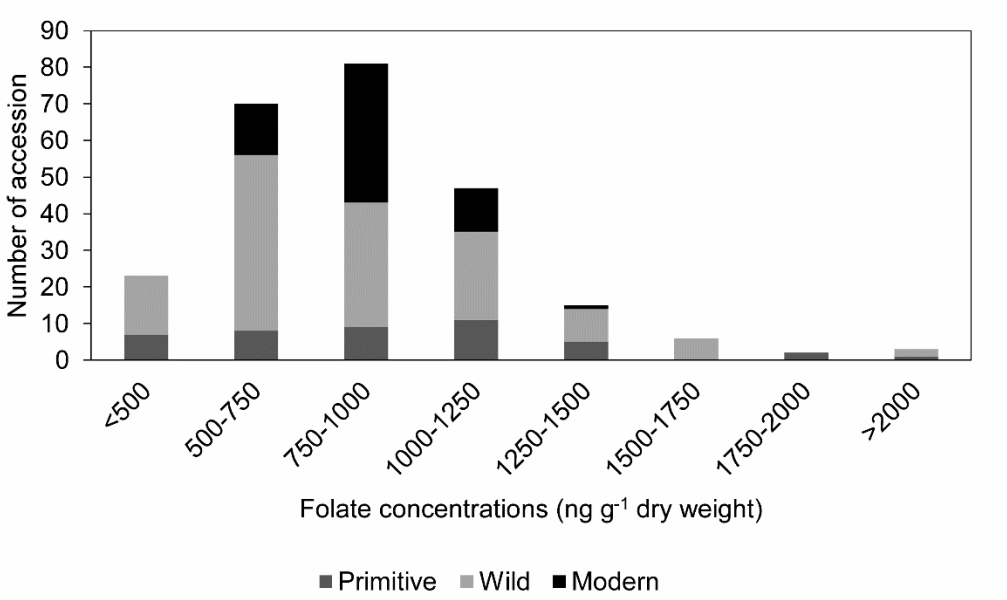

Fig. 1 Number of accessions within folate concentrations brackets. Sixty-five varieties or advanced breeding lines, and 43 and 139 accessions from primitive cultivated and wild species, respectively, were analyzed for folate content as reported before (Goyer and Navarre 2007; Goyer and Sweek 2011; Robinson et al. 2015). For wild species, each accession was made of tubers pooled from four individuals (Goyer and Sweek 2011), or was the average of one to four individuals analyzed independently (Robinson et al. 2015).

Screening of wild relatives or primitive cultivars, that represent a larger gene pool, may be necessary to identify sources of high folate content that are worth integrating in breeding programs for folate enhancement of potato tubers. Therefore, 54 clones from 33 accessions of primitive cultivars (*S. tuberosum* group *Andigenum*) and 62 accessions representing 25 wild potato species were evaluated for folate content (Goyer and Sweek 2011). Two clones of primitive cultivars within accessions PI 225710 and PI 320377 had folate concentrations above 2,000 ng g^{-1} dry weight. Individuals from two accessions of *S. vernei* yielded folate concentrations above 1,500 ng g^{-1} dry weight. More strikingly, individuals from the wild species *S. boliviense* within accession PI 597736 had folate concentrations above 3,000 ng g^{-1} dry weight. These accessions and species were identified as potential sources of the high folate content trait and were further evaluated by extending folate phenotyping to additional individuals within promising accessions and additional accessions within promising species (Robinson et al. 2015). All three previously evaluated species, *S. tuberosum* group *Andigenum*, *S. boliviense*, and *S. vernei*, produced again individuals with folate concentrations close to or above 2,000 ng g^{-1} dry weight. High folate content individuals within *S. tuberosum* group *Andigenum* and *S. boliviense* species were also from the promising accessions identified in the first screening (PI 225710, PI 320377, PI 597736). These results confirmed these species and accessions as good sources of the high folate content trait deserving further scrutiny.

Folate Content is Higher in Developmentally Younger Tubers

An evaluation of folate concentrations in tubers of three russet varieties harvested throughout the growing season from mid-June until the end of September showed that folate content decreases about three-fold during tuber enlargement (Goyer and Navarre 2009) (Fig.2). This trend will

need to be further confirmed in other varieties and other types of potatoes, in particular early season potatoes. Nevertheless, these results suggest that higher consumption of new or baby potatoes could significantly increase folate intake.

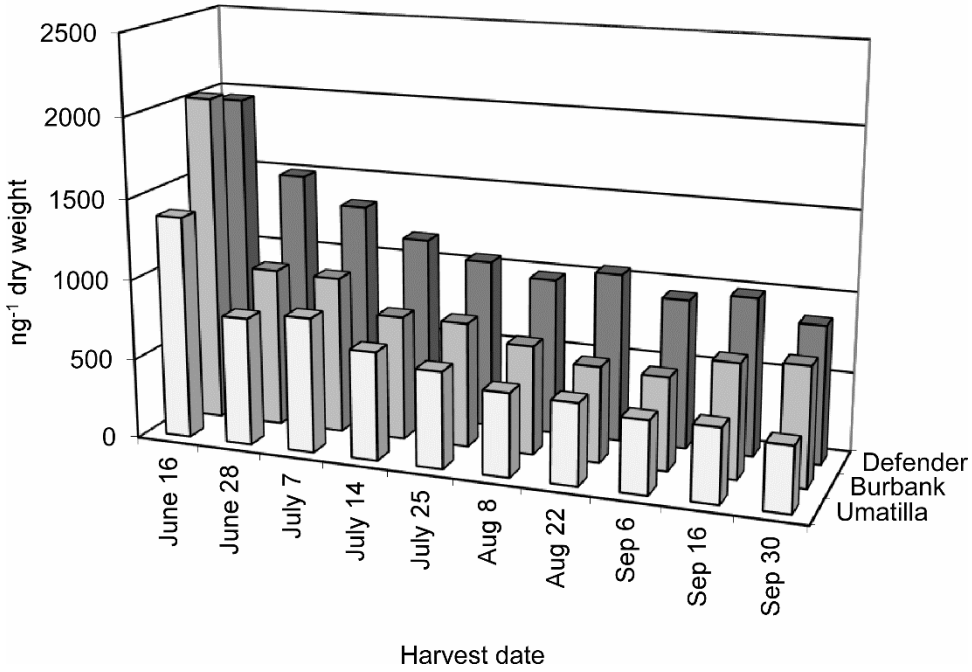

Fig. 2 Folate concentrations in potato tubers harvested throughout the growing season. Modified from (Goyer and Navarre 2009).

Low Temperature Storage Increases Folate Content

Potatoes are often stored at low temperature for several months before going to the market or processing. Interestingly, folate concentrations increase in tubers stored at low temperature (Fig.3). The extent of this increase, which seems to be genotype-dependent, can be as high as two-fold or more. Such treatment could further increase folate intake, especially in countries where cold storage is already inherent in the field-to-plate chain. The effect of cold storage on other micronutrients should be carefully evaluated to assess the full potential of cold treatment on the overall potato nutritional value, as it is well-known that cold storage has the opposite effect on vitamin C (Kulen et al. 2013).

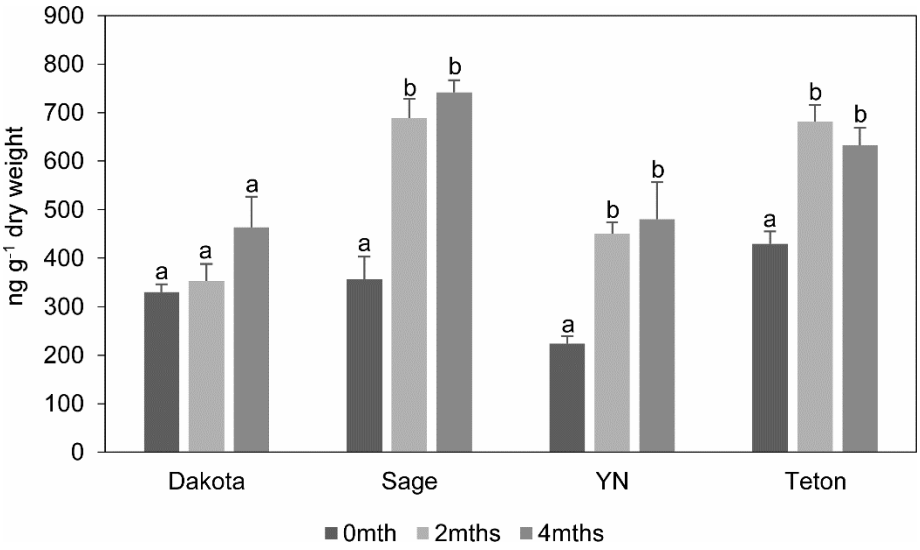

Fig. 3 Folate concentrations in potato tubers at harvest and after two and four months in low temperature storage. Tubers were harvested in 2014 and stored at 9°C.

New Folate Phenotyping Methods are Needed

Several methods exist to quantify folate in plant foods (Quinlivan et al. 2006). A tri-enzyme extraction coupled with a microbiological assay is the most economical technique to evaluate folate in a large number of samples. However, this assay is tedious and time-consuming. New phenotyping methods for folate content are needed to evaluate the large genetic diversity of potato germplasm. To this end, we are using two approaches to identify genes or markers that are associated with folate content. First, the expression of genes involved in folate metabolism was determined in high and low folate *Solanum boliviense* tuber samples using RNA-sequencing (RNAseq) and real time quantitative RT-PCR (qPCR). RNAseq analysis showed that γ-glutamyl hydrolase 1 (GGH1) was consistently expressed at higher levels in high folate compared to low folate segregants of a *S. boliviense* accession (unpublished). QPCR analysis showed that GGH1 transcripts levels were higher in high folate compared to low folate segregants for seven out of eight additional pairs of folate segregants. These results suggest that GGH1 gene expression may be a determinant of folate content in potato tubers. Second, 94 F_2 progeny from an interspecific cross between a high folate *S. boliviense* clone and the low/medium folate recombinant inbred clone USW4self#3 were genotyped using the Illumina Infinium 12808 SolCAP array. Survey SNP trait association and SNP-trait association analyses were performed to identify SNPs and genomic regions associated with high folate content. A total of 497 significant SNPs were identified (unpublished). Further work is needed to validate these results.

Conclusion

Our results showed that there exists a genetic diversity for folate content in potato that could be used in breeding programs for folate biofortification of potato. However, the potential increase in folate content may be limited to approximately two-fold. The question remains whether this is the maximum potential increase possible or whether additional screening of potato germplasm will lead to the identification of individuals with even higher folate content. Our work has

identified species and accessions that consistently yield individuals with high folate content. These species and accessions deserve further exploration for the identification of very high folate sources. Future screening would be facilitated by the identification of genes or markers for folate content that we have started to characterize.

In addition to genetic diversity, we showed that developmental stages and environmental factors such as cold storage have an effect on folate content of tubers. These factors could be used positively by the potato industry to maximize folate content. Considering a 20% dry matter content, an average daily consumption of 150 g of potato (i.e. current potato consumption in the United States), and an average retention rate of 80% during cooking (retention rate varies between cooking and processing methods (Navarre et al. 2009)), most current commercial potatoes provide between 5 and 6% of the recommended daily folate intake (i.e. 400 µg per day) (Fig.4). A combination of approaches (i.e. genetic, consumption of young tubers, and storage at low temperature) could potentially lead to a typical 150 g serving of potato providing 40 to 48% of the recommended daily intake of folate (Fig.4). This positions the potato to play a significant role in eradicating worldwide folate deficiencies.

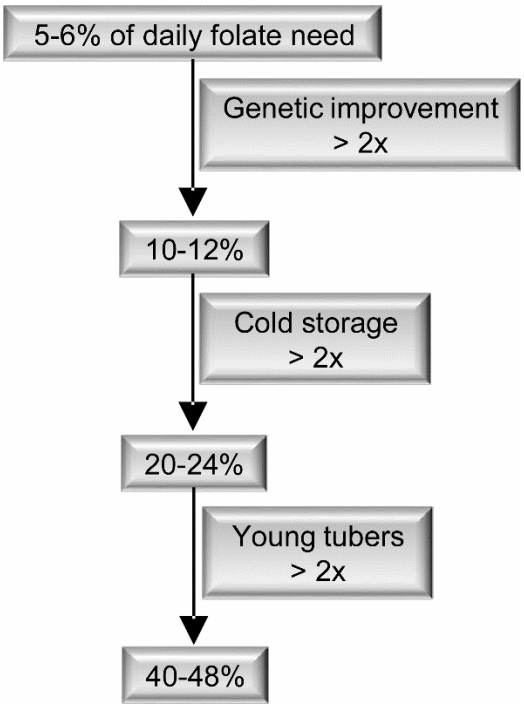

Fig. 4 Diagram showing the percentage daily folate need provided by a medium size modern potato tuber (i.e. 150 g) and the potential increase obtained by combining breeding, postharvest treatment, and selection of developmental stage. An average retention rate of 80% during cooking or processing was used (Navarre et al. 2009).

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