



Potato biofortification: an effective way to fight global hidden hunger

Baljeet Singh^{1,2} · Umesh Goutam² · Sarvjeet Kukreja³ · Jagdev Sharma⁴ · Salej Sood¹ · Vinay Bhardwaj¹

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Abstract Hidden hunger is leading to extensive health problems in the developing world. Several strategies could be used to reduce the micronutrient deficiencies by increasing the dietary uptake of essential micronutrients. These include diet diversification, pharmaceutical supplementation, food fortification and crop biofortification. Among all, crop biofortification is the most sustainable and acceptable strategy to overcome the global issue of hidden hunger. Since most of the people suffering from micronutrient deficiencies, have monetary issues and are dependent on staple crops to fulfil their recommended daily requirements of various essential micronutrients. Therefore, increasing the micronutrient concentrations in cost effective staple crops seems to be an effective solution. Potato being the world's most consumed non-grain staple crop with enormous industrial demand appears to be an ideal candidate for biofortification. It can be grown in different climatic conditions, provide high yield, nutrition and dry matter in lesser time. In addition, huge potato germplasm have natural variations related to micronutrient concentrations, which can be utilized for its biofortification. This review discuss the current scenario of micronutrient malnutrition and various strategies that could be used to overcome it. The review also shed a light on the genetic variations present in potato germplasm and

suggest effective ways to incorporate them into modern high yielding potato varieties.

Keywords Micronutrients · Potato · QTL · GWAS · Transgenics

Introduction

Feeding the world is a massive challenge because the global population is increasing at alarming rates. It is estimated that world population will increase to 9.6 billion by 2050 (Mishra et al. 2018). At present, nearly 800 million people are undernourished (FAO 2017) and around 2 billion people are suffering from micronutrient malnutrition, which is called as hidden hunger (IFPRI 2016; UN General Assembly 2016). Among all the micronutrients, the deficiencies of Zinc (Zn) and Iron (Fe) are widespread. Worldwide 1.6 billion people are Fe deficient (McLean et al. 2009) and about 17% of the global population is Zn deficient (Wessells and Brown 2012; Hefferon 2019). This situation becomes even worse in developing countries like India (Talsma et al. 2017; Harding et al. 2018). Approximately, 50% of the global micronutrient deficient population live in India (Ritchie et al. 2018). During the last decade, a lot of progress has been made to reduce this hidden hunger by various ways such as food fortification, dietary supplements and biofortification (Obersteiner et al. 2016; FAO 2017; Allen and de Brauw 2018).

Crop biofortification has emerged as a powerful tool to combat micronutrient malnutrition. It is a cost-effective approach, which paves its way towards sustainable micronutrient supply to the poor. Since the twenty-first century, a number of biofortified crops have been released worldwide (Garg et al. 2018; Meena et al. 2018). However,

✉ Vinay Bhardwaj
Vinaycpri@gmail.com

¹ Division of Crop Improvement and Seed Technology, Central Potato Research Institute, Shimla, India

² School of Bioengineering and Biosciences, Lovely Professional University, Phagwara, India

³ Department of Agronomy, Lovely Professional University, Phagwara, India

⁴ Division of Crop Production, Central Potato Research Institute, Shimla, India

being the staple food a large portion of world's population depends upon cereals, which however provides insufficient amounts of micronutrients (Pérez-Massot et al. 2013; Garcia-Oliveira et al. 2018). Therefore, to reduce the micronutrient malnutrition globally, there is an urgent need to improve the world's most consumed non-grain food crop 'Potato'. It is already a rich source of micronutrients (Navarre et al. 2016, 2019; Zaheer and Akhtar 2016; Furrer et al. 2018), especially when consumed along with skin (Subramanian et al. 2011). Its biofortification could be a boon for people suffering from hidden hunger. More than 50% potatoes are produced by developing countries (FAO 2009), where the micronutrient malnutrition is highly prevalent (Perez-Escamilla et al. 2018; Wakeel et al. 2018). Thus, importance of micronutrient biofortification in potato becomes high from the human health perspective as it is consumed in high amounts by a larger portion of world population.

Hidden hunger: a silent epidemic

Micronutrients play vital roles in both humans and plants. Their deficiencies may lead to serious health issues in humans and it may cause yield or quality losses in plants (Quintaes and Diez-Garcia 2015; Dimkpa and Bindraban 2016). Insufficient intake of micronutrients by humans is called as hidden hunger (Ritchie et al. 2018). Worldwide, micronutrient malnutrition is somehow associated with more than 50% deaths (Lyons 2018). About 150 million children below the age of five show stunted growth and about 50 million are under weighed (UNICEF 2018). Nearly, 52 million children below five years suffer malnutrition globally, including ~ 36 million children in Asia and 2 million in India (Singh et al. 2015). Hidden hunger is widespread in developing countries and become an abysmal for the poor (Harding et al. 2018). The major reasons exacerbating the hidden hunger are; low monetary resources, lack of diversity in diet, dependence upon high yielding cereals which are often less micronutrient dense (Von Grebmer 2018; Zikankuba et al. 2019). The micronutrient malnutrition due to Fe and Zn deficiencies is most prevalent and have most devastating effects (Bailey et al. 2015). The recommended levels of Fe, Zn, Cu and I required for the ideal functioning of the human body has been compiled in Table 1.

Current strategies to overcome hidden hunger

There are several ways to reduce the hidden hunger, which could be implicated to increase dietary intake of essential micronutrients such as dietary diversification, medical

Table 1 Recommended Daily Allowance (RDA) of Iron (Fe), Zinc (Zn), Copper (Cu) and Iodine (I) for different age groups and genders. *Source* The data for table is obtained from National Institutes of Health (NIH), Office of Dietary Supplements, <https://ods.od.nih.gov/> (Accessed on 08/05/2021)

Age	Iron			Zinc			Copper			Iodine		
	Male	Female	Pregnancy	Male	Female	Pregnancy	Male	Female	Pregnancy	Male	Female	Pregnancy
0–6 months	0.27 mg*	0.27 mg*		2 mg*	2 mg*		200 mcg *	200 mcg *		110 mcg*	110 mcg*	
7–12 months	11 mg	11 mg		3 mg	3 mg		220 mcg *	220 mcg *		130 mcg*	130 mcg*	
1–3 years	7 mg	7 mg		3 mg	3 mg		340 mcg	340 mcg		90 mcg	90 mcg	
4–8 years	10 mg	10 mg		5 mg	5 mg		440 mcg	440 mcg		90 mcg	90 mcg	
9–13 years	8 mg	8 mg		8 mg	8 mg		700 mcg	700 mcg		120 mcg	120 mcg	
14–18 years	11 mg	15 mg	27 mg	11 mg	9 mg	12 mg	890 mcg	890 mcg	1000 mcg	150 mcg	150 mcg	220 mcg
19–50 years	8 mg	18 mg	27 mg	11 mg	8 mg	11 mg	900 mcg	900 mcg	1000 mcg	150 mcg	150 mcg	220 mcg
51 + years	8 mg	8 mg		11 mg	8 mg		900 mcg	900 mcg		150 mcg*	150 mcg*	

* Adequate intake

supplementation, food fortification and crop biofortification (Fig. 1) (Wakeel et al. 2018). The choice of strategies for reducing hidden hunger depends upon several factors such as availability of resources, financial status of target population, sustainability, accessibility and acceptability of consumers. Dependence upon one type of food on regular basis may lead to a specific type of micronutrient malnutrition. Therefore, diet diversification is a simple, effective and natural way to increase micronutrient bioavailability (Gibson and Hotz 2001). For example, adequately diversified dietary intake helps to reduce serious health issues during pregnancy (Agrawal et al. 2015). Diet diversification can be achieved via different strategies; (1) agriculture based (use of diverse vegetables, fruits and other plant based products), (2) animal based (incorporation of different animal based food and/or seafood products into diet) and (3) integration of processed food products (Maqbool and Beshir 2019). However, changing the regional food habits of people is a challenging task. Worldwide, the dietary supplements are used to reduce the effects of

malnutrition. Previous studies have shown that diet supplements are not just to reduce the hidden hunger but these are also used to enhance the performance of athletes (Maughan et al. 2018). A number of physiological disorders related to micronutrient malnutrition can be eradicated by dietary supplementation (Stewart et al. 2015; Petry et al. 2016). However, most of the times dietary supplements cause some adverse side effects too (Wu and Tsai 2016). Moreover, the hidden hunger is highly prevalent in poor, who cannot afford diversified diet and dietary supplements. Thus, government’s financial support is required to make this intervention effective for the poor (Meenakshi et al. 2010).

Food fortification is another way to enhance nutritional value of food by adding vital trace elements and vitamins to it with minimal risk to health (Garrett 2018). Food fortification can be done at industrial level (Mannar and Hurrell 2018) and/or directly at consumer’s plate (Somassè et al. 2018). The foods that are economical, easily available and consumed in high amounts in a region can be targeted

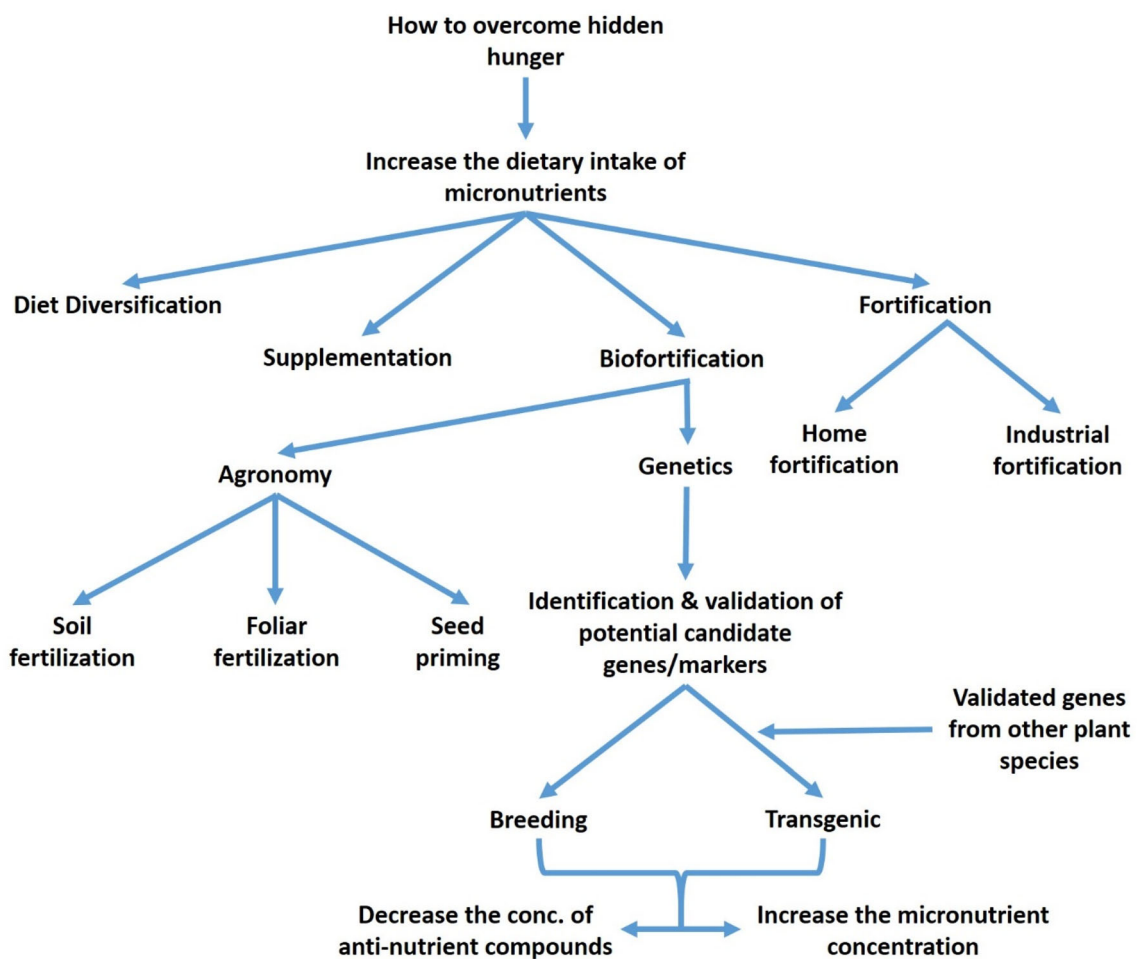


Fig. 1 Different strategies to reduce the burden of global hidden hunger

for industrial fortification. Studies have revealed that, micronutrient powders (MNP) are effective to reduce anaemia and gain weight in children under 2 years of age (Lazzerini 2013; Somassè et al. 2018). This method of food fortification also has some shortcomings. Food fortification with micronutrients may change its quality, flavour, shelf life, colour, appearance and consequently lead to poor consumers acceptance (Habeych et al. 2016; Blanco-Rojo and Vaquero 2019). However, this approach is more economical than the use of pharmaceutical supplements but still the population suffering from micronutrient malnutrition cannot afford it (Bouis 2003).

Improving micronutrient concentrations through biofortification is a cost effective, reliable and sustainable method that could supply micronutrients to the poor in long terms. It is an upcoming approach with tremendous potential to increase the nutritional value of food crops in the fields, rather than adding nutrients artificially into them while processing. Plenty of nutrient rich food crops have been developed successfully through biofortification (Garg et al. 2018; Meena et al. 2018). However, the eradication of micronutrient malnutrition in developing countries where staple crops lack micronutrients is still a big challenge (Pérez-Massot et al. 2013).

Potato an ideal crop for biofortification

Potato is a versatile crop and its biofortification can reduce the micronutrient malnutrition significantly (Fig. 2). It is a staple crop of many countries because it is easy to grow, requires less land than other major crops and provides more nutrients per unit area, time and money (Mullins et al.

2006). It is cultivated under different climates such as temperate, tropical and subtropical regions and its production and consumption has increased tremendously in the developing countries (Zaheer and Akhtar 2016). It is consumed as fresh vegetable and also has massive industrial demand (Furrer et al. 2018). It is naturally a nutrient rich crop (Table 2). Due to its nutritional value potato, became the staple food of many countries. It provides more nutrients in lesser price than most of the other vegetables and fruits (Drewnowski and Rehm 2013). It is a good source of carbohydrate, protein, minerals, vitamins and dietary fibres. As per the nutritional profile, potatoes provide a good quantity of vitamin C, vitamin B6, K, Fe and folate (Robertson et al. 2018). If cooked without peeling off potatoes can provide more nutrients and dietary fibres (Singh et al. 2020a, b; Sampaio et al. 2020). However, the nutritional value may vary slightly from variety to variety. For example, coloured potatoes are a rich source of antioxidants such as polyphenols, β -carotene, carotenoids, anthocyanins and flavonoids (Soare et al. 2020). Some of these compounds remain in significant amounts even after cooking such as anthocyanin (Ercoli et al. 2021).

Recently Jongstra et al. (2020) reported that iron bioavailability in potatoes is very high as compared to the cereals. Andre et al. (2015) used an in vitro gastrointestinal digestion and a CaCO_2 lines based model of human intestine and showed that around 70% of iron released from the potatoes remains available at the intestinal level. Further, only a small amount of Zn from different agricultural foods is bioavailable to humans at gastrointestinal level. The food crops contain various organic compounds some of them favours Zn absorption and some can reduce its bioavailability such as phytic acid (PA). The molar ratio of

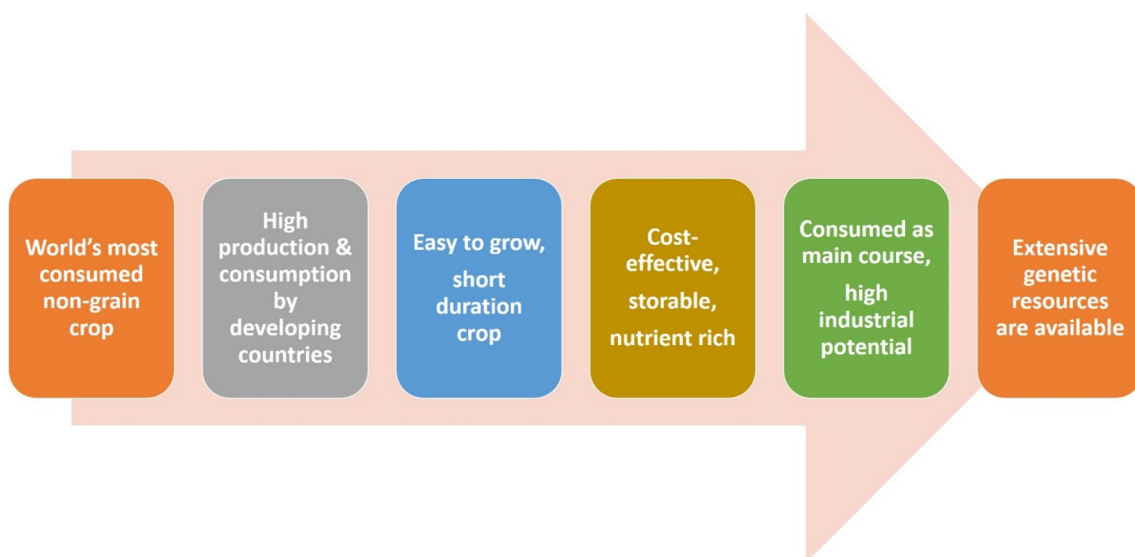


Fig. 2 Major reasons for proposing potato an ideal candidate for biofortification

Table 2 Nutritional profile of raw potatoes with skin (*Source:* United States Department of Agriculture (USDA), Agricultural Research Service (ARS), 2018)

Name	Value per 100 g	38 g skin
<i>Proximates</i>		
Water	83.29 g	31.65 g
Energy	58 kcal	22 kcal
Protein	2.57 g	0.98 g
Total lipid (fat)	0.10 g	0.04 g
Carbohydrate, by difference	12.44 g	4.73 g
Fiber, total dietary	2.5 g	0.9 g
<i>Minerals</i>		
Calcium, Ca	30 mg	11 mg
Iron, Fe	3.24 mg	1.23 mg
Magnesium, Mg	23 mg	9 mg
Phosphorus, P	38 mg	14 mg
Potassium, K	413 mg	157 mg
Sodium, Na	10 mg	4 mg
Zinc, Zn	0.35 mg	0.13 mg
<i>Vitamins</i>		
Vitamin C, total ascorbic acid	11.4 mg	4.3 mg
Thiamin	0.021 mg	0.008 mg
Riboflavin	0.038 mg	0.014 mg
Niacin	1.033 mg	0.393 mg
Vitamin B-6	0.239 mg	0.091 mg
Folate	17 µg	6 µg

PA:Zn is widely used to measure the Zn bioavailability in foods. The Zn bioavailability in potato tubers is high because of the presence of high concentrations of organic compounds, which promote absorption of Zn in potatoes and low concentrations of compounds, which restrain Zn absorption. Therefore, a significant amount of the recommended dietary allowance (RDA) for iron and zinc can be obtained from potatoes. Vergara et al. (2019) successfully increased the Zn bioavailability in potato tubers by priming the tubers in zinc solution.

Moreover, an extensive amount of natural variations for micronutrient content exists in vast potato germplasm (Burgos et al. 2007; Ritter et al. 2008; Haynes et al. 2012; Paget et al. 2014; Subramanian et al. 2017; Singh et al. 2020a, b). These variations can be utilized to develop biofortified potatoes (Fig. 3). The potato germplasm collections are maintained at different locations throughout the world (Table 3). The potato germplasm has a great variation in terms of tuber size, shape, flesh color, skin color, distribution of pigments, skin type, nutrient concentrations and tolerance to biotic and abiotic stresses (Jiménez et al. 2009; Berdugo-Cely et al. 2017; Furrer et al.

2017; de Haan et al. 2019; Singh et al. 2020a, b). Therefore, diverse potato gene pool must have some unidentified genes that might be utilized in the potato biofortification programs. Identification of genes controlling tuber mineral concentration in diverse potato populations will permit the scientists to expand the range of variations in present potato cultivars (Bradshaw et al. 2006; Subramanian et al. 2017). Moreover, potato genome sequence is available publically, which can catalyse the process of biofortification with the help of advance biotechnological tools. Potato biofortification can be done via three different methods viz., agronomical, transgenic and breeding (Garg et al. 2018; Shukla and Mishra 2018).

Agronomical biofortification

Agronomical biofortification involves the seed tuber priming and application of mineral fertilizers to enhance the micronutrient concentrations in the edible portion of food crops (Cakmak and Kutman 2018). Vergara et al. (2019) reported successful zinc biofortification by priming the potato tubers in 10 mg/ml Zn for 12 h. The micronutrient containing mineral fertilizers can be applied to plants via foliar application or through soil application (Poblaciones and Rengel 2016; de Valença et al. 2017). Both soil and foliar application of trace elements have been employed to biofortify the major food crops including potato (Cakmak and Kutman 2018; Lyons 2018). However, foliar application of micronutrient fertilizers is a more efficient approach to improve the mineral content in the edible parts of a crop than the soil application (Zhao et al. 2014; Lawson et al. 2015; Kromann et al. 2017). Previous studies showed that micronutrient spraying on potato plants enhance the micronutrient concentrations in tubers and also increase the tuber yield and dry matter content (Al-Jobori and Al-Hadithy 2014; Kromann et al. 2017; Zhang et al. 2019).

The agronomic biofortification has tremendous potential to increase the nutrient content in potato (Table 4) but on the downside, it has some limitations too. The efficiency of agronomic biofortification depends upon various factors such as soil composition, soil pH, mineral mobility, mineral accumulation, environmental conditions and plant growth stage when the fertilizers are applied (Dimkpa and Bindraban 2016; Garg et al. 2018). It is not an efficient method to increase the bioavailability of nutrients, which are synthesized via plant metabolism. Further in case of Fe, this method is not much effective because Fe is immobilized in soil in ferric form but plants absorb Fe in ferrous form (Pérez-Massot et al. 2013). Moreover, it is a temporary and an expensive way of biofortification, one has to perform the same agronomic practices repeatedly.

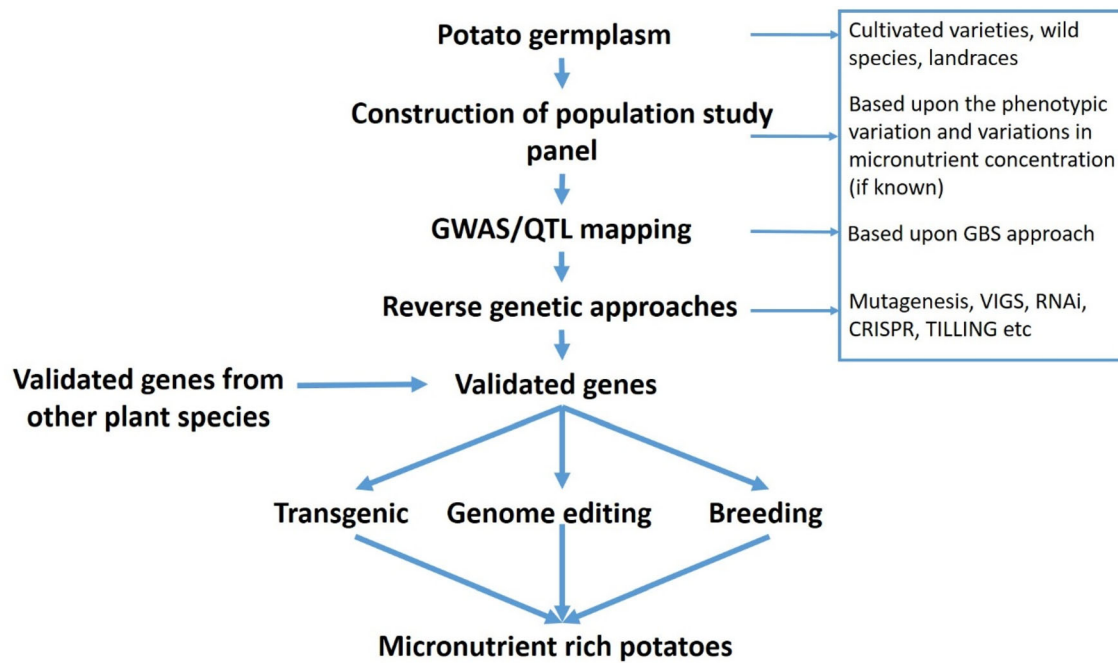


Fig. 3 A systematic flow chart proposing an effective way for the development of micronutrient rich potato varieties

Table 3 Different institutes having collection and maintenance of potato germplasm

Name	Location	Reference
International Potato Centre	CIP, Lima, Peru	https://cipotato.org/genebankcip/
Dutch-German Potato Collection	CGN, Wageningen, The Netherlands	https://www.wur.nl/en/Research-Results/Statutory-research-tasks/Centre-for-Genetic-Resources-the-Netherlands-1/Expertise-areas/Plant-Genetic-Resources/CGN-crop-collections/CGN-potato-collection.htm
The Gross Luesewitz Potato Collections	GLKS, IPK, Groß Luesewitz, Germany	https://www.ipk-gatersleben.de/en/genebank/satellite-collections-north/gross-luesewitz-potato-collections/
The Potato Collection of the Vavilov Institute	VIR, St Petersburg, Russia	Dzyubenko (2018)
US Potato Genebank	NRSP-6, Sturgeon Bay, USA	https://www.ars-grin.gov/nr6/
Commonwealth Potato Collection	The James Hutton Institute (JHI), Dundee, Scotland	https://ics.hutton.ac.uk/germinate-cpc/#home
The Indian Council of Agricultural Research-Central Potato Research Institute	ICAR-CPRI, Shimla, India	https://www.cpri.in/

Transgenic approach

The biofortification of micronutrients using transgenic approach provides sustainability because transgenics produce self-fortifying seeds (Blancquaert et al. 2015). The development of nutrient rich crops using transgenic approach is an efficient and cost-effective method. This approach allows using a broad range of genes associated with different micronutrients from even entirely unrelated

species (Xu et al. 2017; Muñiz García et al. 2018) and can be used to reduce the content of anti-nutrients (Pérez-Massot et al. 2013). Thus, it permits the biofortification of a nutrient, which does not exist in the whole germplasm of a crop. Moreover, tissue specific biofortification can be done using transgenic approach (De Lepeleire et al. 2018). Therefore, the concentrations of micronutrients in the edible part of targeted crop can be enhanced. To maximize the uptake, mobilization and storage of micronutrients in

Table 4 List of different agronomic practices for biofortification of potato

Method	Type of biofortification	Country	References
Foliar application	Se	Italy	Poggi et al. (2000), Cuderman et al. (2008)
Foliar application	Se	Slovenia	Zhang et al. (2019)
Foliar application	Mg, S, Zn, B	India	Ramesh et al. (2019)
Foliar application	cobalamin, folic acid and ascorbic acid	Egypt	Youssif et al. (2017)
Foliar application	Zn, B, Fe, Mn	India	Moinuddin et al. (2017)
Foliar application	Fe, Zn, Mn, Ti	Poland	Wadas and Kalinowski (2019)
Foliar application	urea, humic acid (HA), Zn, B	Pakistan	Shah et al. (2016)
Foliar application	Nanaofertilizer, Seaweed and Hypertonic	Iraq	Al-Juthery et al. (2018)
Foliar application	Fe, Mn, Cu, Zn	Iraq	Al-Jobori and Al-Hadithy (2014)
Foliar application	Zn	United Kingdom	White et al. (2017)
Both Foliar and Soil application	Zn, Fe	United States	Kromann et al. (2017)
Both Foliar and Soil application	Zn, Fe	Bolivia	Gabriel et al. (2015)
Tuber priming	Zn	Brazil	Vergara et al. (2019)

Table 5 Transgenic studies conducted for potato biofortification

Micro-nutrient	Gene(s)	References
Beta-carotene	StLCYb	Song et al. (2016)
Beta-carotene	lycopene epsilon cyclase (LCY-e)	Diretto et al. (2006)
Amino acid composition	AmA1	Chakraborty et al. (2010)
Anthocyanins, phenolic acids	chalcone synthase (CHS), chalcone isomerase (CHI), and dihydroflavonol reductase (DFR)	Lukaszewicz et al. (2004)
Vitamin B9	HPPK/DHPS, FPGS	De Lepeleire et al. (2018)
Vitamin B6	PDX-II gene	Bagri et al. (2018)
Vitamin C	GalUR gene	Hemavathi et al. (2009)
Vitamin C	StVTC2A	Bulley et al. (2012)
Vitamin C	StDHAR	Qin et al. (2011)
Vitamin A	EuCrtB, EuCrtI, EuCrtY	Diretto et al. (2007)
Vitamin A	BoOr	Lopez et al. (2008)
Vitamin A	PaCrtB	Ducreux et al. (2005)
Calcium	Scax1	Park (2005)
Calcium	Cax2b chimeric	Kim et al. (2006)

plants many transgenic studies have been performed in major food crops (Saalbach et al. 2014; Takenaka et al. 2019; Wu et al. 2019). Recently, various attempts have been made by scientists to enhance the potato tuber quality with respect to micronutrients via transgenic approach (Mitchell et al. 2017; Xu et al. 2017; Bagri et al. 2018; Muñiz García et al. 2018). The overexpression of PDXII gene from *Arabidopsis thaliana* in potato under the control of CaMV35S promoter increased the accumulation of vitamin B6 and enhanced abiotic stress tolerance (Bagri et al. 2018). Likewise, incorporation of *Arabidopsis* ABF4

in potato improved the tuber yield, quality and abiotic stress tolerance (Muñiz García et al. 2018). Furthermore, AtMYB12 gene from *Arabidopsis* has increased the content of caffeoylquinic acids and flavonols in potato tubers (Li et al. 2016). Many genes associated with micronutrient acquisition, transportation, accumulation and tolerance have been reported previously (Blancquaert et al. 2017; Kumar et al. 2018; Moreira et al. 2018; Papierniak et al. 2018; Migocka et al. 2019). Legay et al. (2012) reported the elevated expression of several genes including the well-known iron regulators FRO1, FRO2, IRT1, FRD3,

NRAMP, VIT1, FIT/FER in *in-vitro* potato plantlets grown in iron deficient media. As the functions of these genes are known in other non-graminaceous plants, thus their over-expressor transgenic potato lines could be developed to enhance the tuber Fe content in Fe deficient soils. Beside these, manually curated nutrient use efficiency (NtUE)-related genes and quantitative trait loci (QTLs) are available at (Kumar et al. 2018). By using transgenic techniques, nutrient rich crops can be developed. However, despite of numerous successful transgenic studies (Table 5), only few nutrient rich transgenic varieties have been released (Garg et al. 2018). This is because of legal and ethical issues associated with transgenics.

Breeding

The micronutrient concentrations in various staple crops has been increased by conventional breeding experiments without affecting the other agronomic traits. Various attempts have been made to increase micronutrient content in potato through plant breeding approaches (Table 6). However, in potato the traditional breeding programs were primarily focused to increase the crop yield and disease resistance (Kikuchi et al. 2015). Moreover, most of the modern potato cultivars were developed from a limited germplasm brought from Andeans of South America by repeated breeding. Hence, most of the modern potato cultivars have less genetic variability (Fig. 4) (Barrell et al. 2013; Hameed et al. 2018). However, Berdugo-Cely et al. (2017), reported that the potato germplasm present at ‘the colombian central collection’ have great phenotypic and genotypic diversity. By using 4666 SNPs, they find out 23 significant and robust marker-trait associations with different phenotypic traits. Haynes et al. 2012 investigated genetic variations associated with micronutrient concentrations in 18 potato clones and reported significant variations for Fe, Zn, Cu and Mn concentrations in potato. Further, Haan et al. (2019), reported high nutritional diversity for dry matter, energy, protein, iron and zinc content in Andean diverse landraces and modern potato varieties. As the huge pool of ‘potato germplasm’ itself have genetic variations for micronutrient content (de Haan

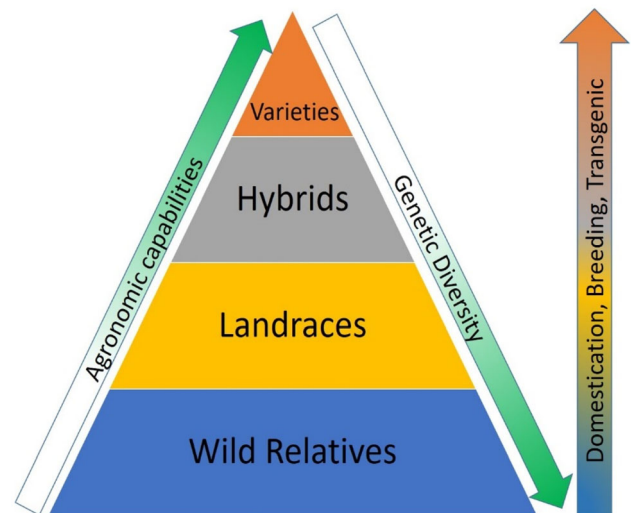


Fig. 4 Pyramid chart depicts the decreased genetic diversity in modern potato varieties due to potato domestication, repeated breeding and transgenic studies performed for better agronomic traits

et al. 2019; Haynes et al. 2012), so it can be biofortified using conventional breeding.

Breeding approaches to increase micronutrient content in potato tubers depends upon environmental conditions and soil composition (Trawczyński 2016; Martins et al. 2018). The genotype x environment interactions (GEI) have significant effect on tuber’s nutritional quality (Mohammed 2017; Haynes et al. 2019). Burgos et al. (2007), reported notable variations in the tuber Fe and Zn concentrations due to GEI when grown at two different locations. Therefore, multi-environmental trials are required to choose potential parents for potato breeding programs and to reduce the effect of GEI (Kelly et al. 2007).

Genetic approaches to speed up potato biofortification

Different strategies can be used in potato biofortification programme to speed up the process such as association mapping, QTL mapping to identify potential candidate genes and reverse genetic approaches to validate their functionality (Fig. 3).

Table 6 List of studies conducted for potato biofortification by plant breeding

Micro-nutrient(s)	Country	Reference(s)
Zn, Fe	Peru	(Burgos et al. 2007)
Fe	United states	(Brown et al. 2010)
Cu, Fe, Mn, Zn	United states	(Haynes et al. 2012)
Fe, Zn, Mg, Mn, Ca	Colombia	(Peña et al. 2015)
Antioxidants	Peru	(Lachman and Hamouz 2005; Andre et al. 2007)

Table 7 List of various studies conducted successfully to identify marker-trait associations for mineral nutrient concentrations in different crops by exploiting the germplasm diversity using association mapping (AM) and genome-wide association mapping (GWAS)

Crop	Nutrient for AM	Population size	No of significant associations	Country	References
Common bean (<i>Phaseolus vulgaris</i> L.)	N, P, K, Ca, Mg, Fe, Zn, and Mn	174 accessions	31 quantitative trait nucleotides	Croatia	Gunjača et al. (2021)
Common bean (<i>Phaseolus vulgaris</i> L.)	Fe, Zn, C, K, Ca, P, and Mg	109 genotypes	NA	India	Jan et al. (2021)
<i>Vigna radiata</i> L.	Ca, Fe, K, Mn, P, S, and Zn	95 genotypes	43 MTAs	United States	Wu et al. (2020)
<i>Phaseolus Vulgaris</i> L.	Fe, Zn Vitamin A	206 genotypes	10 SNP marker trait associations	Mexico	Binagwa et al. (2020)
Rice (<i>Oryza sativa</i> L.)	Fe and Zn concentrations	152	7 QTLs (2 for Fe and 5 for Zn)	Philippines	Descalsota-Empleo et al. (2019)
Wheat (<i>Aegilops tauschii</i>)	Micronutrients (Fe, Zn, Cu, and Mn)	167 accessions	19 SNP marker trait associations	India	Arora et al. (2019)
Rice (<i>Oryza sativa</i>)	Ionic Variation (N, P, K, Ca, Mg, Fe, Mn, Mo, B, Cu, Zn, Co, Na, Cd, As, Pb, Cr)	529 accessions	72 loci associated	China	Yang et al. (2018)
Maize (<i>Zea mays</i> L.)	Fe and Zn concentration	923 inbred lines	46 SNP marker trait associations (26 for Fe and 20 for Zn)	Mexico	Hindu et al. (2018)
Wheat (<i>Triticum aestivum</i> L.)	Zn concentration	369 wheat genotypes	40 SNP marker-trait associations	Germany	Alomari et al. (2018)
Lentil (<i>Lens culinaris</i> subsp. <i>culinaris</i>)	Fe and Zn concentration	96 germplasm lines	7 SSR marker trait associations	India	Singh et al. (2017)
Spinach (<i>Spinacia oleracea</i> L.)	Mineral element concentrations (B, Ca, Co, Cu, Fe, K, Mg, Mn, Mo, Na, Ni, P, S, Zn)	292 accessions	45 SNP marker trait associations	United States	Qin et al. (2017)
Common bean (<i>Phaseolus vulgaris</i> L.)	Micronutrients (Fe, Zn and protein)	96 genotypes	13 SSR marker trait associations	India	Mahajan et al. (2017)
Rice (<i>Oryza sativa</i> L.)	Fe and Zn concentration	222 accessions	60 QTLs (29 for Fe and 30 for Zn)	China	Zhang et al. (2017)
Barley (<i>Hordeum vulgare</i> L.)	Mn concentration	248 barley varieties	54 SNP marker trait associations	Denmark	Leplat et al. (2016)
Potato (<i>Solanum tuberosum</i> L.)	Fe and Zn concentrations	170	11 marker trait associations (4 for Fe and 7 for Zn)	Peru	CGIAR (2016)
Chickpea (<i>Cicer arietinum</i> L.)	Fe and Zn concentrations	92 accessions (39 desi and 53 kabuli)	16 genomic loci (gene-based SNPs)	India	Upadhyaya et al. (2016)
Rice (<i>Oryza sativa</i>)	Mineral Element Contents (Fe, Zn, Se, Cd, Pb)	416 accessions (planted) but only 378 were finally used	20 QTLs	China	Huang et al. (2015)
Rice (<i>Oryza sativa</i> L.)	Mineral Element Contents Zn, Fe, Cu, Mn, P, Ca, K, Mg	219 accessions planted but only 175 were used	60 SSR marker trait associations	China	Nawaz et al. (2015)
Maize (<i>Zea mays</i> L.)	Fe concentration	302 maize inbred lines planted but 267	35 SNP marker trait associations	Germany	Benke et al. (2015)

Table 7 continued

Crop	Nutrient for AM	Population size	No of significant associations	Country	References
Rice (<i>Oryza sativa</i> L.)	As, Cu, Mo and Zn concentrations	312 accessions	17 SNP marker-trait associations	Several countries	Norton et al. (2014)
Chickpea (<i>Cicer arietinum</i> L.)	Fe and Zn concentrations	94 accessions	8 marker trait associations	Canada	Diapari et al. (2014)
Barley (<i>Hordeum vulgare</i> L.) landraces	Fe and Zn concentration	298 accessions	14 SNP marker trait associations	United States	Mamo et al. (2014)
Sorghum (<i>Sorghum bicolor</i> (L.) Moench)	Grain quality traits including Ca and P	300 accessions	8 SNP marker trait associations	United States	Sukumaran et al. (2012)
<i>Arabidopsis thaliana</i>	Mineral Element Contents (B, Na, Mg, P, S, K, Ca, Mn, Fe, Co, Ni, Cu, Zn, As, Se, Rb, Mo, Cd)	96 accessions	Many different associations for different traits	Belgium	Baxter et al. (2012)

Association mapping and QTL analysis

Exploration of desirable genetic variations and their introgression into the modern potato varieties is a big challenge due to high heterozygosity and polyploid nature of potato genome (PGSC 2011). Association mapping (AM) or genome-wide association studies (GWAS) are efficient techniques to screen the fruitful genes and genomic regions associated with a complex phenotypic trait (Ma et al. 2016; Rojas et al. 2019). It provides higher mapping resolution in comparison to linkage mapping population (Huang and Han 2014). So far, these techniques have been employed to screen the genes/markers/QTLs associated with micronutrient contents in various food crops (Table 7). In potato, these have been performed successfully to identify the marker-trait associations for tuber bruising (Urbany et al. 2011; D'hoop et al. 2014), starch content (Schönhals et al. 2016), and glycoalkaloid content (Manrique-Carpintero et al. 2014; Vos et al. 2016). Genotyping by sequencing (GBS) based GWAS experiment was performed on a panel of 170 potato landraces with genetic variations for Fe and Zn content. They found four genetic markers significantly associated with Fe content and seven with zinc content (CGIAR 2016). However, the genetic basis of micronutrient content in potato is still poorly known and demands further investigation of genetic variations linked to micronutrient content (Haynes et al. 2012).

Reverse genetic approaches

GWAS, QTL mapping and by utilizing different bioinformatics approaches potential candidate genes/markers/QTLs associated with micronutrient content can be identified. However, functional validation of these potential candidates is important before their incorporation into any potato cultivars, which can be done by reverse genetic approaches. For an instance, virus induced gene silencing (VIGS) is a simple, rapid and efficient method to study the gene function by suppressing its expression (Bekele et al. 2019). The role of ferric reductase oxidase (*FRO1*) gene has been verified in *Nicotiana benthamiana* using tobacco rattle virus (TRV) based VIGS (Gama et al. 2017). This technique has been successfully applied to validate the functionality of various candidate genes in potato (Cui et al. 2009; Zhong et al. 2018). Generation of transfer (T)-DNA mutants is also a fast and effective way to study the candidate gene's function (Radhamony et al. 2005; Duangpan et al. 2013). This technique can also be employed in potato to develop T-DNA mutant lines for any specific gene (An et al. 2005; Duangpan et al. 2013). In addition, other reverse genetic techniques such as RNA interference (RNAi) (Aggarwal et al. 2018), clustered regularly interspaced short palindromic repeats (CRISPR) (Klimek-Chodacka et al. 2018; Martín-Pizarro et al. 2019), zinc finger nucleases (ZFNs) (Petolino 2015) and targeting induced local lesions in genomes (TILLING) (Chen et al. 2014; Sánchez et al. 2018) can also be employed for the same reason. In the last decade, CRISPR-Cas9 based genome editing has been extensively used for crop improvement (Yin et al. 2017; Langner et al. 2018; Singh et al. 2018). It involves a guide RNA (gRNA) of about 20

nucleotides (spacer sequence) complementary to the target gene and a Cas9 endonuclease enzyme that has the ability to generate double stranded breaks (DSB) 3–4 bases after the protospacer adjacent motif (PAM). These DSB later on gets repaired either by error prone non-homologous end-joining pathway (NHEJ) or by homology directed repair pathway (HDR) (Zhao et al. 2016; Jiang and Doudna 2017).

Conclusion

Overcoming the hidden hunger is very crucial for a large portion of world population. Although several approaches are available but biofortification seems to be a highly sustainable approach. Dietary diversification, pharmaceutical supplementation and food fortification are not affordable for poor. Thus, these are less sustainable methods than crop biofortification. Potato crop gives significant response to agronomic practices such as tuber priming, use of soil and foliar fertilizers but farmers should be aware of dose and time of fertilizer application to get the best benefit of it. Moreover, understanding of genetic basis of micronutrient concentrations in potato tubers can facilitate potato biofortification. Wide range of genetic diversity for mineral concentration exists in potato germplasm that can be utilized via genetic engineering and plant breeding to develop nutrient rich potato varieties. However, due to ethical and biosafety issues the development of biofortified transgenic potatoes is less efficient approach to reduce hidden hunger in comparison to plant breeding. Although, traditional breeding experiments are time consuming, but nowadays with the help of advance biotechnological tools more precise and accurate breeding programs can be designed to improve micronutrient concentration in potato.

Future perspective

During the last decade, genetic engineering and genome-editing techniques, advance biotechnological, bioinformatics tools, and new breeding technologies have been mushroomed up because of their application potential. Earlier, these technologies were focused to improve the quantitative traits in potato (Hameed et al. 2018). However, to reduce the hidden hunger these techniques individually or in combination should be applied to improve the tuber micronutrients concentrations. Various attempts have been performed successfully to improve the mineral concentrations, vitamin and protein content, beta-carotene, and antioxidants levels. To catalyse the potato biofortification programs a better understanding of various pathways associated with the mineral elements uptake, accumulation

and assimilation is required, which can be achieved by using advanced tools. Many genes associated with micronutrient concentrations are validated in model plants and in major food crops including potato. The potential genes from other species can be introduced to potato cultivars via genetic engineering. The expression of positive regulatory genes can be enhanced in potato and the genes that promote biosynthesis of anti-nutritional compounds can be knocked down via genome editing techniques or gene silencing approaches. The techniques namely ZFNs, transcription activator-like effector nucleases (TALENs) and CRISPR offer precise genome editing. These techniques provide a potential alternative of transgenic approaches, as these do not involve the permanent insertion foreign genes. CRISPR-Cas9 technique can be successfully applied to potato with the help of geminivirus replicons (GVRs) (Butler et al. 2016; Nadakuduti et al. 2019). Potato is responsive to plant tissue culture based propagation (Bamberg et al. 2016), thus it is comparatively easy to develop nutrient rich superior non-GMO potato plants for future with these approaches.

However, vast potato germplasm itself have many unknown genes that can increase the content of mineral elements in it. With the advent of next generation sequencing (NGS) techniques and availability of potato genome sequence, the genetic variations underlying the mineral composition can be investigated through GBS based GWAS technique. This technique provide potential candidate genes/markers associated with an observable trait that can be later validated by reverse genetic approaches. After validation, breeders can use them to speed up the development of biofortified potato varieties through marker-assisted selection (MAS) breeding and precision breeding. Previously most of the breeding experiments in potato were based upon phenotypic characters but now with the help of GWAS, these can be planned on the basis of genotypic variations. However, for the development of stable phenotypes understanding of GEI is also important. Ultimately, all these advanced biotechnological tools and high-throughput sequencing methods will lead to the development of nutrient rich potato varieties and help to diminish the grave problem of hidden hunger especially in the developing world.

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