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BIOFORTIFICATION IN POTATOES: A SYSTEMATIC REVIEW

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ABSTRACT: Crop biofortification has emerged as a powerful tool to combat micronutrient malnutrition. It is vital to address the issue of hidden hunger in light of the expanding global population. Across the world, biofortification is a workable, economical, and sustainable way to meet the nutritional needs of the weaker segments of society. Malnutrition, specifically hidden hunger, is an international phenomenon. Individuals with mineral deficits who are unable to afford a diversified diet or dietary supplements may benefit from biofortified variants. To satisfy the nutritional requirements, an integrated approach incorporating breeding, biotechnology, and agronomy would be implemented. Unlike dietary diversification, nutritional supplementation, and fortification, biofortification requires a one-time investment for the development of biofortified varieties, with recurring costs comparable to those of any crop variety now in use. The potato crop responds well to agronomic techniques, but maximising the benefits of these techniques requires knowledge and understanding. Potato biofortification can also be facilitated by knowledge of the genetic basis of the micronutrient concentrations in potato tubers. Potato germplasm has a broad range of genetic variability for mineral concentration, which can be used in crop breeding to create potato cultivars that are high in nutrients. Though conventional breeding takes a lot of time, more precise breeding strategies can be designed to improve the nutritional components of potatoes with the use of the latest tools like DNA free gene editing.

KEYWORDS: Potatoes, Nutrition, Biofortification, Breeding Approaches, Nutrition security

With a net productivity of 25.79 tonnes per hectare and a total production of around 60.14 million tonnes from a planted area of 2.33 million hectares, India ranks as the second largest potato producer in the world (2022-23) (Sources: https://agriwelfare.gov.in; Department of Agriculture & Farmers Welfare, 2022-23 Final). The latest (2022) global annual production of potatoes is 375 million tonnes, with an average productivity of 21.1 t/ha (2022; FAOSTAT), and thus average productivity of potatoes in India is higher than that of the world's average potato productivity. India alone produces nearly 14% potatoes of the total world potato production. It is anticipated that the medium and long-term observed changes in Indian socioeconomics will increase per capita fresh potato consumption from 19.78 (2010) to 48.47 kg by 2050 and corresponding national food demand for fresh potatoes will be 38.2 and 78.5 million tonnes during 2025 and 2050, respectively (Vision 2025). As a result, biofortified potatoes may be able to

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meet a large portion of the general public's nutrient needs.

Nutritional components of potatoes

Potato tubers contain on an average of 80% water and the rest of the proximate composition is constituted by starch, protein, fibres, free sugars, fat, vitamins, minerals and phytonutrients (Table 1). Though potato is a starchy crop under high-GI category food and is viewed as a less healthy dietary option; however, there are many aspects to consider about the value of potato in the human diet (Sagili *et al.*, 2022). Post-harvest processing can have a major effect on the GI/GL values of potatoes and is a good source of instant energy for the undernourished people. The potato proteins have a very high biological value (BV) of 90 (Egg protein has a biological value of 100 and is considered the reference protein) and are comparable/better to soybean with a BV of 84 and beans with a BV of 73 (McGill *et al.*, 2013). Better protein quality can be very useful, especially to malnourished populations. Potato is one of the rich sources of Vitamin C, Potassium and Folate (Raigond *et al.,* 2023). Therefore, despite having carbohydrate rich potato has several nutraceutical components to make it one of the options to fight hunger and malnutrition.

However, potato tuber contains many more phytochemicals, which have nutraceutical properties. Phenolics and flavonoids, including carotenoids, anthocyanins, and flavonols, are the primary phytochemical components found in potatoes and there are genotypic differences in the content of these phytochemicals and usually colored skin/fleshed potatoes are richer in anti-oxidant compounds as compared to white skin/fleshed ones (Ezekiel *et al.*, 2013). It has been demonstrated that potato genotypes with pigmentation-primarily purple and red cultivars-contain noticeably larger quantities of antioxidants than those with white or yellow flesh (Kulen *et al.,* 2013; Stushnoff *et al.*, 2008). These chemicals can counteract oxidative cell damage and provide protective or disease-preventive qualities. Thus, they may aid in the prevention of age-related neuronal degeneration, cancer, and chronic illnesses. Phenolics, which are among these phytochemicals, are known to provide both health advantages and organoleptic qualities. Chlorogenic acid accounts for around 80% of the total phenolic content in potatoes (Brown, 2005). Following apples and oranges, potatoes rank as the third most significant source of phenols, with about half of the phenols concentrated in the peel and adjacent tissues (Freidmen, 1997). Anthocyanins, which are also critical antioxidants, are found in coloured potatoes. A subset of flavonoids is responsible for the red, blue, and purple hues of potato flesh and skin. The presence of acylated glycosides of pelargonidin results in the red hue, while acylated glucosides of malvidin, petunidin, peonidin, and delphinidin impart a purple hue (Brown, 2005). These substances enhance the overall appearance and promote the health and well-being of consumers by inhibiting the oxidation of LDL-cholesterol and safeguarding human cells from the damage caused by free radicals. Potatoes also contain carotenoids, in white-fleshed potatoes the values are 5–10 mg kg^{-1} FW,

Table 1. Nutrient content of potato per 100-gram fresh weight

Nutrient (unit)	Content	Nutrient (unit)	Content
Carbohydrates (g)	17	Phosphorus (mg)	57
Fat (g)	0.09	Zinc (mg)	0.29
Protein (g)	2.0	Copper (mg)	0.11
Fiber (g)	2.2	Manganese (mg)	0.15
Calcium (mg)	12	Vitamin C (mg)	19.7
Iron (mg)	0.78	Vitamin B complex (B1, B2, B3, B5, B6) (mg)	0.03-1.05
Potassium (mg)	421	Vitamin B9 (µg)	16
Magnesium (mg)	23	Vitamin A (IU)	2

while yellow-fleshed potatoes have 10–35 mg kg^{-1} FW. Lutein, zeaxanthin, violaxanthin and neoxanthin are the major carotenoids present in potatoes, whereas β-carotene is present in trace amounts (Tatarowaska *et al*., 2019). Cultivars differ in these carotenoids' ratios. Despite not being precursors to vitamin A, all xanthophylls are powerful antioxidants. Zeaxanthin and lutein are responsible for the orange and yellow colours of the tuber flesh, respectively. In addition to providing possible protection against chronic illnesses and some types of cancer, lutein/zeaxanthin has been implicated in preventing age-related macular degeneration and shielding the retina from blue light damage (Ezekiel *et al*., 2013).

Potato-A perfect crop for biofortification

A crop with great versatility, potatoes are grown in over 150 nations from Chile to Greenland, right from temperate to sub-tropical and tropical climates, from sea level to 4,700 metres above sea level. Potatoes are more efficient than cereals in productivity per unit of area and water used (Kanter and Elin, 2019). Potatoes are much-admired for their role in alleviating hunger and reducing malnutrition and are marketed as a nutritious food because they contain antioxidants and other health beneficial compounds. Potato is the only noncereal staple food ranked fourth after grain crops. The bioavailability of iron (Fe), zinc (Zn), potassium, vitamin C, vitamin B6, and folates is higher than that of cereal crops due to lower phytic acid content and higher ascorbic acid content (Rashid *et al*., 2024). Potatoes are ideally suited for biofortification since potato cultivars have high ascorbic acid to phytate ratio, which may be considered appropriate for mineral fortification for targeted mineral delivery since phytate inhibits mineral absorption while ascorbic acid promotes their absorption in the gut (Joshi *et al*., 2021). With its maximum variation among the agronomic and quality traits, the potato has great potential especially for micronutrient biofortification (Rashid *et al*., 2024). Potato is also a good source of resistant starch. In several ways, natural resistant starch supports a healthy colon (Leeman *et al*., 2006). One approach to this shift is biofortification, which is based on the idea of improving nutrient composition through breeding techniques.

Health benefits of biofortified potatoes

The use of food-based strategies to avoid chronic diseases is becoming more and more popular (McGill *et al*., 2013). Additionally, potatoes are becoming more and more well-known as a source of minerals and bioactive phytochemicals (Brown *et al*., 2003; Thompson *et al*., 2009). In addition to their antioxidant properties, phenolic compounds may have other health-promoting properties. Numerous research investigations examined the anticancer, antiproliferative, and antioxidant properties of potato polyphenols (Singh *et al*., 2008, Kaspar *et al*., 2010, Madiwale *et al*., 2012). Of all the phenolic compounds, phenolic acids have sparked the most interest due to their possible health advantages (Mattila *et al*., 2007). Potato tubers with higher concentrations of chlorogenic acid have been shown to enhance insulin sensitivity, reduce intestinal glucose absorption, and inhibit gluconeogenesis (Andre *et al*., 2014; Ong *et al*., 2013). In a six-week study, Kaspar *et al*. (2010) examined the impact of eating potatoes with pigment on inflammatory damage and oxidative stress in men. The findings demonstrated that eating potatoes with yellow and purple flesh decreased DNA damage and inflammation. Increased consumption of potatoes, which are rich in anthocyanins, was correlated with lower plasma concentrations of C-reactive protein, a biomarker for the course of disease (Kaspar *et al*., 2010). Some of the hepatic antioxidant enzymes expressed more and antioxidant potential in the serum and liver increased in rats, when purple potato flakes were fed to them (Han *et al.*, 2007). Additionally, rats' hepatic superoxide dismutase mRNA was increased by red potato flakes, enhancing the antioxidant system (Han *et al.*, 2007).

Potato polyphenols also have certain other positive health effects that may not be related to antioxidants (Andre *et al.*, 2008). For example, potato extracts reduced the proliferation of breast (Leo *et al.*, 2008) and colon (Madiwale *et al.*, 2012) cancer cells, with the latter case also demonstrating pro-apoptotic characteristics (Roleira *et al.*, 2015). Potato anthocyanin compounds inhibited the growth of benzopyrene-induced stomach cancer in rats (Madiwale *et al.*, 2012, Hayashi *et al.*, 2006). Higher phenolic content extracts showed stronger cytotoxic and antioxidant properties (Roleira *et al.*, 2015). Given that potatoes are widely consumed worldwide, they may therefore be a perfect source of phytochemicals that promote health.

Factor affecting the nutritional quality of potatoes

The stability and concentration of phytochemicals in the human diet are subject to various influences, including genotype, agronomic conditions, post-harvest storage, cooking and processing (Ezekiel *et al.*, 2013).

Variety: From variety to variety, the nutritional content may differ slightly (Luthra *et al.*, 2018a). The amount of protein in 100 grams of potatoes can range from 1 to 4.2 grams on a fresh weight (FW) basis, depending on the variety (McGill *et al.*, 2013). Antioxidants such as flavonoids, anthocyanins, polyphenols, and β-carotene are abundant in coloured potatoes (Soare *et al.*, 2020) and phenolic content may vary upto fifteen times (Navarre *et al.*, 2009). Andre *et al.*, (2007) documented that the concentration of total carotenoids in 74 Andean landraces varied from 3 to 36 μg/g DW. Brown *et al.* (2007) conducted a study on 38 native South American potato cultivars, selected for coloration of skin and flesh combined with high dry matter, and assessed the antioxidant values and total anthocyanins. The results revealed that the concentrations of total anthocyanin varied from undetectable to 23 mg cyanidin equivalents/100 g FW, total carotenoid levels varied from 38 to 2020 μg zeaxanthin equivalents/100 g FW, hydrophilic oxygen radical absorbance capacity (ORAC) values ranged from 333 to 1408 μM Trolox equivalents/100 g FW and lipophilic ORAC values ranged from 4.7 to 30 nM-tocopherol. Total anthocyanins and total carotenoids have been reported to be negatively correlated (Li *et al.*, 2022). Recently, Dalamu *et al.* (2023) found substantial diversity for anthocyanins (1.81–17.20 mg/100 g FW), ascorbic acid (14.50–85.00 mg/100 g FW), carotenoids (4.75–27.75 μg/g FW), and total phenolics (19.22–73.54 mg GAE/100 g FW), tuber dry matter content (14–26 percent), iron (30.49–56.29 ppm), and zinc (10.62–27.58 ppm based upon the nutritional investigation of 71 potato genotypes. According to the study's findings, two genotypes-the indigenous Kala Aloo line and the Andigena line JEX/A-122 may be utilised as parents to develop potato varieties with better nutraceutical values. There is large variability in the potato germplasm concerning tuber size, shape, flesh colour, skin colour, pigment distribution, skin type, nutrient concentrations, and resistance to biotic and abiotic stresses (de Haan *et al.*, 2019; Singh *et al.*, 2020b). A diversified gene pool for potatoes must therefore contain undiscovered genes that could potentially be employed in potato biofortification initiatives. The ability to increase the diversity of existing potato cultivars will be facilitated by the identification of genes regulating tuber mineral concentration in various potato populations (Bradshaw *et al.*, 2006; Subramanian *et al.*, 2017). Furthermore, the potato genome sequence is publicly accessible, which provides the genomic resources to accelerate the biofortification process.

Luthra *et al.* (2018a) found that there was a positive correlation between tuber dry matter content and soluble protein (0.76), ascorbic acid (0.51), and total free amino acid (0.83), and a negative correlation between tuber yield and total protein (-0.75) and ascorbic acid (-0.59). According to Dalamu *et al.* (2023), there was a negative association between tuber yield for anthocyanin (r = -0.46; -0.43), total carotenoids (r = -0.47; -0.38), ascorbic acid (r = -0.27; -0.24), and tuber dry matter (r = -0.21, -0.24). Thus, there always a need to strike a balance between yield and biofortification.

***Environment*:** The impact of environmental conditions on crop quality and yield is a major challenge to breed for the enhancement of a specific trait (Nzaramba *et al*., 2013). The productivity and quality of crops are impacted by environmental circumstances, which encompass phytonutrient levels (Payyavula *et al*., 2012) and potato tuber specific gravity (Davenport, 2000; Sterrett *et al*., 2003). The strategies employed in breeding to enhance the micronutrient content of potato tubers are contingent upon the soil composition and environmental circumstances. Foliar application of micronutrient fertilizers has been used to fortify raw potatoes for the contents of iron and zinc (Ierna *et al.,* 2020). Genotype × environment interactions (GEI) exert a substantial influence on the nutritional quality of the tuber (Mohammed 2017; Haynes *et al*., 2019). Burgos *et al*. (2007) showed significant discrepancies in the contents of Fe and Zn in tubers cultivated at two distinct locations as a result of GEI. To limit the impact of GEI and select potential parents for potato breeding programmes multi-environmental experiments are necessary (Kelly *et al*., 2007).

Storage: Besides the genotype, environment and cultural practices; maintenance of nutritional composition during storage is also one of the desirable characteristics of biofortified potatoes. Since potatoes are around 80% water and 20% dry matter, they are a semi-perishable commodity and must be kept in a regulated environment to be consumed for an extended period for round the year supply for fresh market as well as processing industry consumption. In India, nearly 90% of potatoes are produced in winter and stored during long hot summer. Potatoes used for seed, table and processing are kept under refrigerated conditions., The nutritional content of stored potatoes is affected by the storage temperature and conditions used. According to the findings of Rosenthal and Jansky (2008), the antioxidant activity of preserved tubers was greater than that of fresh tubers. Total phenols increased during storage, with the rise being greatest at 4°C and 16°C, according to Ezekiel and Singh (2007), who examined the effects of storing four cultivars at 4, 8, 12, 16 and 20°C for 180 days. It has been found that irradiated potatoes contain a greater quantity of total phenols following storage at 10, 20, and 30°C (Thomas, 1982) and 5 and 20°C (Mondy and Gosselin, 1989). After analysing the anthocyanin content of tubers from 14 genotypes both immediately after harvest and after 135 days of storage at 4°C and 86 percent relative humidity, Jansen and Flamme (2006) did not see a statistically significant alteration in the tuber anthocyanin content. A five-month storage study of potatoes in Sweden demonstrated that the amount of vitamin C decreased by 60% and the amount of vitamin B6 increased by 20%. The levels of potassium, thiamine and other vitamins and minerals were unchanged (Ohrvik *et al*., 2010). After seven months of cold storage at 4°C, all potato cultivars had a mean decline in vitamin C concentration up to 52%, while two coloured varieties had a modest rise in total polyphenol content (Kulen *et al*., 2013).

From various studies, it may be deduced that the storage temperature and storage environment including relative humidity, gaseous composition etc. impacts potato nutrition content. Therefore, biofortification improvement programmes should aim at developing potato varieties with minimum losses of nutrients upon long term storage under prevailing storage practices of the region.

Processing: The potato processing industry in India is currently expanding at a rapid rate as a result of the growing urban working population, the universal acceptance of potato processed products, and the availability of specialised varieties for processing (Gupta *et al.*, 2020). Currently, processing accounts for about 8.9% of all potato yield; by 2025, that percentage is expected to rise to 10.76 percent (CPRI Vision, 2050). Tubers should have a high dry matter content (> 20 percent) and low reducing sugars (ideally < 0.1 percent on a fresh weight basis) to be used for high-quality dehydrated products (flakes, flour, powder, etc.) or fried products (chips or French fries) (Kumar and Ezekiel, 2006). Dehydrated chips, cubes, and other items are also easily made at the small-scale industrial level, which can give employment to rural youth and village women (Luthra and Gupta, 2019). In addition, potatoes are used in the production of other processed foods including tikkis, Alu Bhujia, dried chips, and samosas.

To produce the final product with additional value, potatoes must go through multiple processing steps. Depending on the operation involved, nutrient losses are known to occur to varied degrees. Traditional potato processing methods like chuno lead to a nutritional loss in potatoes (Woolfe, 1987). One of the main concerns when processing potatoes into different products is the loss of nutrients, which must be kept to a minimum. When potatoes are dehydrated into products like potato flour, flakes, granules, and dice, nutritional value is lost in the process. Changes in phytochemicals and the activation of certain enzymes that alter the concentration of phenolic compounds can result from processes such as handling, washing, and slicing (Tudela *et al.*, 2002). It has been demonstrated that cutting fresh potatoes can alter their phenolic component and antioxidant content (Reyes *et al.*, 2007). According to Reyes and Cisneros (2003), the wounding reaction is genotypically specific and raises the phenolic content and antioxidant capacity of purple-flesh potatoes while decreasing total soluble phenolics and antioxidant capacity in white-flesh potatoes by 15% and 51%, respectively (Reyes *et al.*, 2007). A potato can accumulate polyphenols during the process of slicing. Vahteristo *et al.* (1997) noted a folate content that was 35 to 52 percent lower in French fries compared to the folate content reported by Konings *et al.* (2001) for fried and raw potatoes. Temperature, pH, and the presence of proteins, enzymes, and metallic ions all impact the stability of anthocyanins throughout the processing stage (Rein, 2005).

The breakdown of anthocyanin was reportedly induced by thermal processing (Patras *et al.*, 2010). The anthocyanins undergo enzymatic degradation when exposed to polyphenol oxidase, which can be rendered inactive with gentle heating or blanching (Enaru *et al.,* 2021). Due to their high oxidation susceptibility, anthocyanins and other phenolic compounds become sensitive to oxidative destruction at numerous processing stages (Patras *et al.,* 2010). In comparison to raw potatoes, the hydrogen oxygen radical absorbance capacity (HORAC) and total anthocyanin content of chips and French fries were notably diminished (Brown *et al.*, 2008). In general, potato processing diminishes the antioxidant content. The anthocyanin concentration is diminished more significantly by boiling than by microwave cooking or frying. Potatoes that have been cooked without peeling may retain more minerals, and other nutrients and have higher dietary fibres as compared to peeled potatoes (Singh *et al*., 2020a; Singh *et al*., 2020b; Sampaio *et al*., 2020). Anthocyanin and other nutritional components persist in substantial quantities even after cooking (Ercoli *et al*., 2021). Anthocyanins and carotenoids retain their antioxidant activity even after being subjected to standard cooking methods (Brown, 2005). The impact of cooking on total anthocyanins and HORAC was investigated by Brown *et al*. (2008) in four genotypes whose flesh contained different concentrations of anthocyanins. Total anthocyanins were retained throughout boiling and microwaving but were reduced during baking and frying. According to Navarre *et al.* (2010), efforts to enhance the phytonutrient content of potatoes will be ineffective if the desired phytonutrients are not cooked to a suitable degree. Since potato peels are known to contain a lot of phenolics, boiling and baking potatoes in their skins is thought to be a beneficial cooking technique since it helps to maintain the majority of the nutrients. According to a study by Mattila and Hellstrom (2007), peeled and cooked potatoes had a reduced phenolic concentration in comparison to raw potatoes. In their study, Barba *et al.* (2008) observed substantial reductions in the phenolic content of peeled and unpeeled potatoes, as well as boiled and baked potatoes. A variation in phenolic concentration was documented by Takenaka *et al.* (2006) during the processing stage. This variation was attributed to several factors, including phenolic loss by leaching into water, degradation caused by heat, oxidation by polyphenol oxidase, and isomerization. Baking at 170 °C was shown to greatly reduce total phenolic levels, whereas boiling for 30 minutes and microwave cooking exhibited the least reductions (Stushnoff *et al*., 2008). The phytonutrient losses resulting from baking, boiling, frying, and microwaving were compared by Blessington *et al*. (2010). Boiling potatoes were shown to have a lower carotenoid level than raw potatoes; other cooking techniques did not significantly differ from one another. There was a noticeable drop in quercetin content after baking, boiling, frying, and microwaving (Blessington *et al*., 2010). Tudela *et al*. (2002) reported a comparable drop in quercetin derivatives.

According to Jongstra *et al*. (2020), potatoes have a significantly higher iron bioavailability than cereals. By employing an in vitro gastrointestinal digestion assay and a $CaCO_2$ line-based model of the human gut, Andre *et al*. (2015) demonstrated that around 70% of the iron that was liberated from the potatoes remained accessible at the intestinal level. Due to the presence of large amounts of organic molecules that facilitate zinc absorption in potatoes and low concentrations of chemicals that inhibit zinc absorption, zinc bioavailability in potato tubers is high. Consequently, potatoes provide a substantial portion of the recommended daily intake (RDA) for zinc and iron. Vergara *et al*. (2019) effectively enhanced the zinc bioavailability in potato tubers through the implementation of a zinc solution priming technique.

According to Singh *et al*. (2022), the higher nutrient concentrations in entire tubers as opposed to tuber flesh indicate that these nutrients are mostly found in the tuber's peripheral layers, where peeling the tubers off causes nutrient loss. Peeling off the tubers caused the greatest loss in Fe (35.63%), which was followed by Cu (22.80%), Mn (21.69%), Ca (21.27%), Mg (12.89%), K (12.75%), Zn (10.13%), and Mo. (9.87%).

The losses can be mitigated somewhat by boiling the potatoes with their skins, rather than peeling them (Robertson *et al.*, 2018). The cooking methods that do not involve water, preserve more of the water-soluble vitamin and mineral content (Finglas *et al.*, 1984). Han *et al*, (2007) reported lower vitamin C losses when potatoes were baked (<51%), microwaved (<33%), and sautéed (<67%) than boiled (<88%). It's interesting to note that the vitamin C loss was somewhat decreased to 61-79 percent when salt was added to the boiling water.

Biofortification in potatoes

Nutrient deficiencies resulting from unbalanced dietary practices, and limited access to balanced food options, particularly among impoverished populations, constitute a significant public health concern in both developed and developing nations. Diverse methods of nutrition supplementation each have advantages and disadvantages (Agrawal *et al.*, 2024). Biofortification, which operates on the idea of increasing the nutrient density of food crops through means of plant breeding, biotechnological interventions, or physical application of mineral micronutrient fertilisers to the crop canopy or soil, is one such method. Scientific evidence supports the viability, usefulness, and economics of crop biofortification as a strategy to mitigate nutritional deficiencies. Potato varieties cultivated and consumed throughout Europe and South America are far more diverse, yellow fleshed and are generally regarded as having a more natural flavour (Walker, 1996). The objective of the potato biofortification breeding effort in India is to increase the concentrations of iron and zinc, as well as antioxidants (carotenoids and anthocyanins), in future potato varieties (Luthra *et al.*, 2020a).

Biofortification is an economically viable method of enhancing the nutritional content of food items that are frequently deficient or insufficient in essential elements. This approach primarily addresses the nutritional needs of marginalised communities residing in distant areas, where the execution of alternative nutrient supplementation initiatives is predominantly impeded by inadequate infrastructure. For biofortification programmes to be successful, it is crucial to have a nutrient-dense variety that is well-adapted, popular among farmers and consumers and leads to a marked improvement in the population's health. When the programme is coupled with initiatives to raise community awareness of nutrition and dietary practises, it becomes more successful. Biofortification concentrates on two strategies i.e.: i) biofortification of staple crops to capitalise on the large amounts of food staples that are consistently consumed daily by all members of the family, including women and children who are most vulnerable to micronutrient malnutrition; and (ii) targeting the impoverished mass with low income.

Biofortification is a complementary approach to dietary diversity and other interventions that target micronutrient shortages, like supplementation and fortification, rather than the exclusive means of enhancing micronutrient intakes. Biofortification is a successful strategy to reduce malnutrition in several studies on efficacy (biological impact under controlled conditions similar to clinical trials) and effectiveness (biological influence in real life) (Bouis and Saltzman, 2017).

Breeding for nutritional improvement

Potato is an optimal food for the enrichment of phytonutrients, given that its phytonutrient content can be inherited *via* breeding approaches (Nzaramba *et al.*, 2007). Global breeding programmes are currently raising the amounts of phenolics and/or carotenoids to increase the antioxidant content of potatoes (Andre *et al*., 2007; Reddivari *et al*., 2007). Thus far, the primary emphasis of Indian potato breeding endeavours has been on enhancing both productivity and resistance to diseases and pests. With the introduction of nutrient content as a criterion for cultivar promotion and the development of specialty potatoes, greater emphasis should be placed on breeding potatoes that are rich in nutrients. Exploring the current biodiversity is therefore the initial stage in the development of nutrient-dense potatoes.

Genetics of coloured potatoes

Due to their antioxidant properties, carotenoids and anthocyanins are good for human health. Potato skin or flesh colour varies due to the presence of anthocyanins. The presence or lack of these pigments is regulated by many genes. Chromosome 2 contains the genes that regulate the production of red pigment, whereas chromosomes 11 and 4 have the genes that produce blue and purple pigment, respectively (Brown, 2005). Potato skin and flesh colour distribution is governed by intricate genetic regulation. A single gene determines whether anthocyanin is present or absent, but the distribution pattern is multigenic (Brown *et al.,* 2003). The primary regulatory allele governing the yellow and white flesh colour of potato tubers is the Y locus on chromosome 3, which controls the monogenic inheritance of carotenoids in tubers (Bonierbale *et al*., 1988). An *Or* allele at the Y locus, which is dominant over Y and y, which control yellow and white flesh, respectively, is responsible for the orange flesh (high zeaxanthin). Modifying genes has been linked to regulating the amount of total carotenoids (Brown *et al*., 2006). According to Wolters *et al*. (2010), the dominant allele of beta-carotene hydroxylase (Chy2 allele3) is responsible for the yellow flesh phenotype. The primary element influencing the functional quality of potatoes is genotypic variation (Toledo and Burlingame, 2006). Parra-Galindo *et al*. (2019) identified seven quantitative trait loci (QTLs) regulating anthocyanin concentration in potato tubers on chromosomes 1, 2, 10, and 11. Zhang *et al.* (2009) identified QTLs determining the extent of flesh pigmentation on chromosomes 5, 8, and 9. Yellow-flesh factor (Y/y), which is found on chromosome 3, is the monogenically inherited component that causes the cream, white, yellow, or orange tuber flesh colour due to variable carotenoid content. For marker aided breeding, candidate genes linked to QTLs must be identified. Kloosterman *et al*. (2010) identified the β-carotene hydroxylase (bch) gene linked to the flesh colour of yellow tubers by mapping the gene underlying a significant QTL for flesh colour on chromosome 3. Potato tubers with orange flesh are produced when the homozygous recessive Zep allele coexists with the dominant Bch or Chy2 allele (Wolters *et al*., 2010). Humans need trace amounts of iron and zinc, which are essential for many metabolic activities. Due to their high anthocyanin content, coloured potatoes have the potential to be used as a natural colouring alternative for food products, as they are considered to provide health benefits over banned dyes (Hejtmankova *et al*., 2009).

Multigenic inheritance is observed for mineral characteristics. All 12 chromosomes have minor QTLs for zinc and iron, indicating that breeding to increase these qualities genetically necessitates combining a variety of genes that contribute to the traits (Pandey *et al*., 2023). Studying the processes behind plant mineral uptake, homeostasis, and gene identification related to mineral accumulation is necessary for mineral biofortification. Tuber mineral concentrations are also influenced by some physiological processes. For example, the slow mobility of tuber zinc in the phloem limits the amount of this element in the tuber (Pandey *et al*., 2023).

Targeted nutrients for biofortification of potatoes

Carotenoids, anthocyanins and micronutrients like iron and zinc are the nutrients that are the focus of the Indian potato biofortification initiative. Carotenoids are mostly found in higher content in yellow fleshed potatoes, whereas antioxidants such as anthocyanins are found in larger levels in purple and red potatoes. Antioxidants have been linked to several significant health-promoting activities, including provitamin A activity, immune system augmentation, decreased risk of cancer or cardiovascular disease, and assistance in preventing atherosclerosis (Fakhri and Farzaei, 2022). Anaemia, or iron deficiency, is a major public health issue in India that affects 50-70% of the population, including infants and young children, adolescent boys and girls, women of childbearing age, and pregnant women. It is common in both urban and rural areas. Deficiency of zinc results in pneumonia, respiratory tract infections, and diarrhoea. A severe zinc shortage results in anorexia, cognitive impairment, skin diseases, hypogonadism, and compromised immunological function. Zinc deficiency accounts for around 4.4% of child mortality in developing countries under the age of five (5.3 percent in Africa and 3.7 percent in Asia. One of the main dietary issues in underdeveloped nations is vitamin A deficiency. Clinical and subclinical vitamin A deficiencies are quite prevalent (62 percent) in India, resulting in 330,000 fatalities annually (Akhtar *et al*., 2013).

Strategy for potato biofortification

In India, majority of potato is consumed as vegetable and the potatoes with white skin and white or yellow flesh are consumed by majority of population. In some parts of Bihar and Uttar Pradesh, red skinned potatoes are preferred. Biofortification can be accomplished through genetic (conventional breeding), agronomic, and biotechnological methods.

(i) Breeding approach: In general, conventional breeding programmes for potatoes are mainly concerned with increasing crop productivity and disease resistance. There is less genetic variability for nutraceuticals traits in modern potato cultivars since they are bred using a limited number of germplasm (Barrell *et al*., 2013; Luthra *et al*., 2020a). So far, the majority of breeding efforts have been concentrated on creating potato types with white/yellow flesh that are resistant to biotic and abiotic stressors. The availability of different germplasm enables us to boost potato breeding to generate biofortified varieties, as the *Solanum* germplasm is a rich source of numerous features.

Some of the possible approaches for developing biofortified potato varieties with improved nutritional value have been listed below:

Characterization of potato germplasm including wild species: Germplasm evaluation serves as the preliminary stage in determining the existing variability in populations, which will serve as the foundation for subsequent enhancements. Significant variations can be observed in the shape and colour of tubers (skin/flesh) among potatoes (Fig. 1). There are around 5,000 identified potato cultivars, all of which are members of the genus *Solanum* and species *tubersoum*. Furthermore, eight other *Solanum* species, namely *S. ajanhuiri*, *S. juzpeczukii*, *S. curtilobum*, *S. chaucha*, *S. stenotomum*, *S. phureja*, *S. hygrothermicum*, and *S. goniocalyx*, which serve as a gene pool for the specified nutrients.

All coloured potatoes contain carotenoids (Fig. 2). While the carotenoids in white and yellow skinned potatoes are identical,

Fig.1. Variation for tuber shape and colour of skin/flesh in potatoes

Fig.2. The contrasting intense tuber and flesh colour, yellow colour for carotenoid contents and red/purple colour for anthocyanins

the yellow colour is caused by a larger concentration of xanthophylls. The main type of carotenoids found in potato flesh are called xanthophylls. The carotenoid concentration of the tubers of a hybrid population of diploid potatoes (*S. Phureja* and *S. stenotonum*) was as high as 1435 μg 100 g^{1} FW, the main carotenoids were lutein-5,6-epoxide, violaxanthin, and lutein, followed by neoxanthin, zeaxanthin, and an unknown carotenoid. On the other hand, in the tetraploid clones, violaxanthin is the most abundant carotenoid, accounting for 40% of the total, followed by lutein, lutein-5, 6-epoxide, neoxanthin and zeaxanthin (Lu *et al*., 2001). All potato cultivars have carotenoids in their flesh, although depending on the colour of the flesh, the concentration might differ between cultivars, ranging from 50 to 2000 μg per 100 g FW (Hejtmankova *et al*., 2013). Brown *et al*. (2008) reported a range of 50-100 μg/100g FW in white fleshed varieties, 100-350 μg/100g FW in moderately yellow fleshed varieties and above 1,000 μg/100g FW in intense yellow varieties. Dalamu *et al*. (2017) reported a mean carotenoid content of 98.23 μg/100g FW with a range of 59.71-227.28 μg/100g FW in an investigation on 32 genotypes grown under Indian climatic conditions. Luthra *et al.* (2018b) investigated 64 progenies of cross between Bareilly Red and CP3770 and identified advanced clones like MSP/15-26 and MSP/15-44 (yellow flesh with red vascular ring), MSP/15-56 (yellow flesh with red vascular ring/medulla, multi-coloured chips) MSP/15-51 (red purple flesh), and MSP/15-64 (purple red scattered flesh) having superiority for nutritional components and were considered potential clones for use as elite germplasm for developing superior genotypes under speciality potato sector in India. The mean carotenoid content in flesh was 1060 µg/100g FW, and it ranged from 551 (MSP/15-56) to 1550 (MSP/15-64) in comparison to the parents Bareilly Red (1450) and CP3770 (1500 µg/100g FW).

The Yellow Potato (Papa Amarilla) of the short-day South American Andes has high levels of zeaxanthin (carotenoids) ranging from 800 to 2,000 µg per 100 g FW. The coloured potatoes have also been associated with greater iron levels (Andre *et al.,* 2007; Brown 2008). The bio-accessibility of iron in potatoes is 63 to 79%, which is significantly higher than wheat, common bean, and pearl millet (<30%) (Andre *et al.,* 2015). Burgos *et al.* 2023 found that the absorbed iron from the iron biofortified potato meal was higher as compared to non-biofortified potato meal. Thus, the selection of yellow tuber fleshed germplasm with high iron content is the selection yardstick for breeding iron rich genotypes along with yield advantage, agronomic superiority and wider adaptability.

Presently, the ICAR-Central Potato Research Institute, Shimla in India maintains a modest collection of around 5000 accessions. More than 1000 lines have been screened for ascorbic acid and nearly 300 germplasm lines have been screened for other components like anthocyanin, carotenoids, iron and zinc etc. Around 100 germplasm accessions have been shortlisted from indigenous/exotic sources in the germplasm repository of the institute with one or more nutritional components.

Hybridization to develop biofortified progenies and evaluation of generated progenies: The breeding scheme for the development of nutrient rich potatoes has been described by Luthra *et al.* 2020a. The technique of hybridization entails mating selected nutrient-rich germplasm with variants of improved agronomic traits and wider adaptability to produce a variety of segregating progenies with higher nutritional values (Fig. 3). In single hill seedling generation, the segregating progenies produced are assessed, and clones with acceptable tuber characteristics are chosen. Seedlings and initial clonal generations are cultivated in a zone with low aphid populations, which are vectors for viruses. Cross-breeding diploid and tetraploid varieties can be used to introduce desirable traits, including higher levels of micronutrients

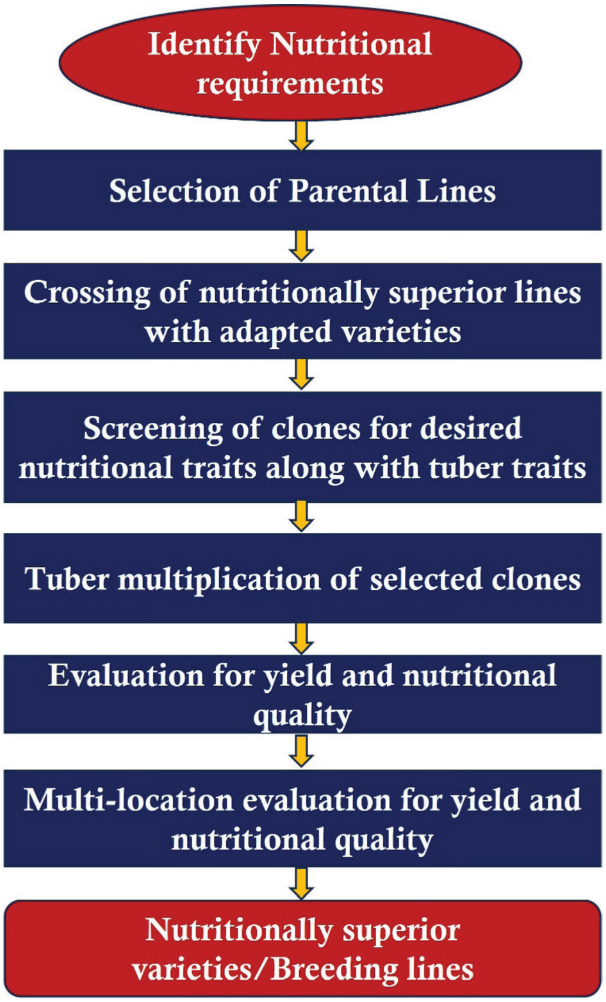

Fig. 3. Breeding Scheme for Development of Nutritionally Superior Varieties

like iron and zinc (Agarwal *et al.,* 2024). The selected tetraploid clones are evaluated in initial clonal stages (F_1C_1, F_1C_2), where the selection of clones is based on shape, colour of skin and flesh, tuber size/uniformity, bulking capacity and targeted nutritional/ mineral components etc. In the F_1C_3 stage, the selection is based on yield advantage (10% better over best control) along with nutritional components. In advanced stage trials, the selection is done based on desirable tuber attributes and nutritional components.

The traditional method of potato biofortification has several drawbacks, including poor heritability of the trait, linkage drag associated with the trait, limited genetic variability accessible for a given nutrient, and a lengthy (10-12 year) period between initial hybridization and variety release.

(ii) Biotechnological approaches: Approaches for genetic modification are especially useful when the desired characteristic is absent from the current germplasm or there is a need to develop genotypes in a relatively shorter time with minimum undesirable traits. Sustainability is provided by the transgenic method of micronutrient biofortification since the seeds produced by the transgenics are self-fertile (Blancquaert *et al*., 2015). This strategy can be used to lower the amount of anti-nutrients (Perez Massot *et al.*, 2013) and is an effective and economical way to leverage a wide variety of genes linked to various micronutrients from even completely unrelated species (Xu *et al*., 2017). Through gene modification, the "golden potato" was created, resulting in increased levels of lutein (30-times), β-xanthophylls (nine-fold), α-carotene, and β-carotene (>3000 fold over the wild type) (Chitchumroonchokchai *et al*., 2017). Researchers have demonstrated the use of transgenic manipulations for crop improvement to enhance beta-carotene's value through RNAi-based silencing of the beta-carotene hydroxylase gene (bch); overexpression of the strawberry GalUR gene to produce anthocyanins and ascorbic acid; coexpression of cystathionine γ-synthase genes to produce essential amino acids like methionine; expression of Amaranth albumin (ama1) genes to increase protein and methionine content in tubers; and role of microRNA (miR828) in purple/red potatoes, among other transgenic manipulations. Under the control of the CaMV35S promoter, the overexpression of the *Arabidopsis thaliana* PDXII gene in potatoes increased vitamin B6 accumulation and improved resistance to abiotic stress (Bagri *et al*., 2018). In a similar study, Muniz Garcna *et al*. (2018) found that adding Arabidopsis ABF4 to potatoes increased tuber yield, quality and resistance to abiotic stress. However, transgenic crops come with some drawbacks, such as strict biosafety regulations and low public acceptance, among others. Future developments in genome editing technology, however, might resolve these problems. To increase beta-carotene level, the potent pro-vitamin A metabolite, the beta-carotene hydroxylase (*BCH*) gene can be targeted. In one of the studies, silencing of *BCH* by using RNAi lead to tubers with more than 300 μg of beta-carotene per 100 g fresh weight (Tuncel and Qi, 2022). Vitamin C contents in tubers were increased up to three-fold when polyubiquitin promoter was used to express GDP-L-galactose phosphorylase (*GGP* or *VTC2A*) gene that is responsible for catalyzing the first committed step of ascorbate biosynthesis in plants (Bulley *et al*., 2012).

Due to the potato genome's high heterozygosity and polyploidy, the investigation of favourable genetic variations and their introgression into present potato cultivars is extremely difficult (PGSC-Potato Genome Sequencing Consortium, 2011). Efficient methods for identifying the beneficial genes and genomic loci linked to traits of interest include genome-wide association studies (GWAS) and genomic selection (GS) (Rojas *et al.*, 2019). These have been effectively implemented in potatoes to determine the relationships between traits and markers, including tuber bruising (Urbany *et al.*, 2011), starch content (Schonhals *et al.*, 2016) and glycoalkaloid content (Vos *et al.*, 2016). Nonetheless, the genetic underpinnings of the micronutrient composition of potatoes remain obscure, necessitating additional research into genetic polymorphisms for various nutritional traits (Haynes *et al.*, 2012).

(iii) Agronomic approaches: To increase the micronutrient concentrations in the edible part of food crops, agronomical biofortification entails priming seed tubers and applying mineral fertilisers (Cakmak and Kutman 2018). It directs the physical addition of nutrients to the soil or foliage, which will improve the food crops' nutritional makeup and, eventually, the nutritional condition of the humans who eat those crops, albeit only momentarily. The mineral fertilisers containing micronutrients can be applied in the soil or foliar to plants. The foliar application of micronutrient fertilisers is a more effective method of increasing the mineral content of a crop's edible portions.

Potato plants that were sprayed with micronutrients had higher tuber yields and dry matter contents in addition to higher micronutrient concentrations in the tubers (Zhang *et al.*, 2019). Numerous variables, including soil composition, pH, mineral mobility, mineral accumulation, weather circumstances, and plant growth stage at the time of fertilizer application; affect agronomic biofortification (Garg *et al.*, 2018). Sharma *et al*. 2022 reported that the bioavailability of Zn from potatoes is high, therefore, the soil application of Zn fertilizers during the initial crop growth stage can be adopted as a simple strategy to increase its content in tubers for addressing Zn-related malnutrition issues.

Furthermore, adding soil microorganisms such as *Rhizobium*, *Bacillus*, *Azotobacte*r, and *Pseudomonas* increases the phyto-availability of mineral elements from the soil to plant edible sections and thus improves the nutritional status of the plants. There exist certain instances of potato biofortification using agronomic interventions, such as foliar zinc treatments that raise the concentration of zinc in entire potato tubers. Even though agronomic biofortification is a straightforward, efficient method, there are strict safety considerations that must be taken about the source of nutrients and how they are applied to prevent toxicity. Affordability and accessibility of fertilisers for farmers with limited resources are further challenges.

Food Security to nutritional security in India

Potatoes have become a staple in the country's households ever since their introduction in the early 17th century, more than four centuries ago, most likely by Portuguese traders. Presently, potatoes are cultivated across all states of India, thriving in a variety of agroclimatic conditions that span from temperate highlands to subtropical plains. In India, the utilization of indigenous and exotic genetic resources has resulted in the development and release of 73 indigenous potato varieties suitable for different agro-ecologies and 46 elite genetic stocks have been registered with ICAR-NBPGR (Luthra and Kumar, 2024). Traditionally, white, cream or yellow skin potatoes are normally favoured in India; however, consumers also exhibit a preference for red skin potatoes in the eastern regions of the country and Jammu and Kashmir. A stronger antioxidant capacity of coloured potatoes may be more desirable for human consumption. Further, they offer diversification of potato dishes in Indian food.

So far three nutrient dense (biofortified) potato varieties namely Kufri Manik (Kumar *et al*., 2023) and Kufri Neelkanth (Luthra *et al*., 2020b) and Kufri Jamunia (Recommended for release by the 41st Group Meeting of AICRP (Potato) held during October 16-18, 2023 at CCS HAU, Hisar, Haryana) have been released in India (Fig. 4). Kufri Manik produces attractive, deep red, round shaped tubers with medium eyes and yellow flesh. Kufri Manik is a nutrient dense variety by virtue of high anthocyanin (68 µg/100g FW), Zinc (33 ppm), and Iron (30 ppm). Kufri Neelkanth has excellent storage qualities and yields visually appealing ovoid tubers that are purple, have shallow eyes, and have flesh that is pale yellow. It is well-known that potatoes, with their purple skin and yellow flesh, contain more anti-oxidants, such as carotenoids and anthocyanins, which help humans fight off a variety of diseases (Luthra *et al*., 2019; Luthra *et al*., 2020b). Kufri Neelkanth possesses higher carotenoids (351 ug/100 g fresh tuber weight, FTW) in the edible part (flesh) and higher anthocyanins in whole tuber (flesh+peel) (84.81 mg/100g FTW). Kufri Jamunia with a total tuber yield of 32-35 t/ha produces attractive purple oblong tubers with shallow eyes and purple flesh. It has 17-19% tuber dry matter, medium tuber dormancy and very good keeping quality (Unpublished). Kufri Jamunia possessed high ascorbic acid content (51.52 mg/100 g fresh tuber weight in flesh) as compared to nutritional superior potato varieties Kufri Manik (37.99) and Kufri Neelkanth (29.04). The purple flesh colour is known to indicate superiority of genotypes for high anthocyanin content and Kufri Jamunia with purple flesh colour possessed higher anthocyanin content (32.36 mg/100 g fresh tuber weight in flesh) than Kufri Manik (26.66) and Kufri Neelkanth (1.12). Kufri Jamunia possessed high carotenoid content (163.04 ug/100 g fresh tuber weight in flesh) as compared to Kufri Manik (99.20) and Kufri Neelkanth (107.52). Kufri Jamunia also possessed at par zinc (22.77 ppm) and iron (32.23 ppm) content on a dry weight basis with Kufri Manik and Kufri Neelkanth. It is suitable for table potatoes and due to its purple colour will add novelty in the preparation of various dishes.

Beside three elite potato genetic stocks namely MSP/16-26 (INGR22062, high carotenoids in flesh (823ug/ 100g FW), **y**ellow flesh colour with red vascular ring); MSP/16-51 (INGR22063, High ascorbic acid in flesh (68 mg/100gFW), distinct red purple flesh) and MS/8-1148 (INGR23120, High vitamin C content (77.7 mg/100g FTW)) has been registered by NBPGR, New Delhi.

Incorporation of nutrient dense traits in breeding population has led to identification of nutrient dense advanced potato clones namely MSP/15-60 (coloured baby potatoes, high anthocyanins:35 mg/100g FW-whole tuber, carotenoids:435 ug/100g FW-flesh, ascorbic

Fig. 4. Biofortified potato varieties released by the ICAR-CPRI, Shimla

acid:44 mg/100g FW-flesh); MSP/16-216 (Multi-coloured chips, high anthocyanins:31 mg/100g FW-whole tuber, carotenoids:176 ug/100g FW-flesh, ascorbic acid:37 mg/100g FW-flesh, and flavouring compounds-AMP+GMP: 4.34 ug/g); MSP17-300 (Purple skin/flesh colour, high anthocyanins:87 mg/100g FW-whole tuber, carotenoids:339 ug/100g FW-flesh, ascorbic acid:32 mg/100g FW-flesh and flavouring compounds-AMP+GMP:4.43 ug/g); MSP/17-375 (purple skin/flesh, high anthocyanins:204 mg/100g FW-whole tuber, carotenoids:370 ug/100g FW-flesh, ascorbic acid:43 mg/100g FW-flesh and flavouring compounds: AMP+GMP-4.75 ug/g); MS/17-739 (high yield, high vitamin C: 45 mg/100g FW, high Fe: 37/44 ppm-flesh/whole tuber); MS/17-848 (multi-coloured flesh, high anthocyanins: 152mg/100g FW on whole tuber, vitamin C: 45 mg/100g FW) in flesh, high zinc:25/28ppm and iron: 38/46 ppm on a flesh/whole tuber).

In India, the breeding programme aiming to develop biofortified potatoes is progressing well and around 1000 nutritionally superior clones are available in various stages of the breeding programme. Recently, screening for lower glycemic index and higher resistant starch has been started and in years to come, we may be able to provide potato varieties having these desirable attributes.

FUTURE THRUSTS

The potatoes are healthful food that, when consumed in sufficient amounts, meets all dietary requirements for nutrients. Any dish made with potatoes has varying nutritional value depending on how it is cooked and what else is included. The development of nutrient-dense potato cultivars is imperative, particularly in light of the growing per capita consumption of potatoes in India (Vision 2050). In this context, initiatives have been launched, and populations up to advanced generations have been created and will soon be distributed as “Nutrient Rich Potatoes” (CPRI Annual report 2018-19). However, for the commercial and economic viability of these nutrient rich potatoes yield advantage, better keeping quality, culinary properties as well as disease and pest resistance are to be taken care of. Further fine mapping of QTLs for nutrient compounds, identification of candidate genes and a better understanding of biosynthesis pathways of these nutrient elements is required for the deployment of functional markers.

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CONFLICT OF INTEREST

The authors declare that they have no conflict of interest.

ETHICAL STATEMENT

This article does not contain any studies with human participants or animals performed by any of the authors.

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