

REVIEW

Prospects to improve the nutritional quality of crops

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Abstract

A growing world population as well as the need to enhance sustainability and health create challenges for crop breeding. To address these challenges, not only quantitative but also qualitative improvements are needed, especially regarding the macro- and micronutrient composition and content. In this review, we describe different examples of how the nutritional quality of crops and the bioavailability of individual nutrients can be optimised. We focus on increasing protein content, the use of alternative protein crops and improving protein functionality. Furthermore, approaches to enhance the content of vitamins and minerals as well as healthy specialised metabolites and long-chain polyunsaturated fatty acids are considered. In addition, methods to reduce antinutrients and toxins are

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presented. These approaches could help to decrease the 'hidden hunger' caused by micronutrient deficiencies. Furthermore, a more diverse crop range with improved nutritional profile could help to shift to healthier and more sustainable plant-based diets.

KEYWORDS

crop improvement, health, nutrient composition, plant breeding, plant-based food, protein content

1 | INTRODUCTION

Selective crop breeding and innovative farming practices have revolutionised modern day crop production in terms of increased yield, hardiness and biomass production. Worldwide, most human caloric intake requirements are supplied by only 15 different crops out of approximately 320,000 currently recognised plant species. Just five crops, rice, maize, sugarcane, barley and wheat, account for more than half of this consumption alone (FAO, n.d.-a; Ross-Ibarra et al., 2007). To meet the growing calorie demand of an expanding population, in the last century, agronomists focussed on large-scale production, intensive irrigation, fertiliser and pesticide use, combined with breeding efforts that aimed for increasing yield and hardiness (Pingali, 2007; Voss-Fels et al., 2019; Yang et al., 2013). An inadvertent side effect of this focus on increased production, however, has been a loss in nutrient quality in staple crops in terms of diversity and quantity of micronutrients as well as their bioavailability when consumed (Davis et al., 2004; Welch & Graham, 2002). Consequently, many staple crops produced today, while meeting the caloric requirements of human diet, fall short in meeting the respective micronutrient demands, resulting in deficiencies also referred to as 'hidden hunger' (Muthayya et al., 2013; de Valença et al., 2017).

Food demand is projected to increase by 40%–70% by 2050 (FAO, 2009, 2017). Simultaneously, climate change and environmental degradation are expected to exert further stresses on crops, calling for the development of crop varieties with an increased tolerance to a plethora of biotic and abiotic stresses (Haberl et al., 2010; Hunter et al., 2017). This is especially challenging as a vast amount of genetic diversity present in ancestral crops has been lost in the process of domestication. Balancing growing calorie requirements in a sustainable manner without losing nutritive value or crop diversity is becoming ever more urgent. Furthermore, especially in high income countries, there is a growing societal trend towards more plant-based food, with an emphasis on plant-produced proteins (Aschemann-Witzel et al., 2020). According to WHO

and FAO as well as many national dietary guidelines, a plant-based diet is both healthier and more sustainable (Bechthold et al., 2018; FAO & WHO, 2019; Herforth et al., 2019; Willett et al., 2019). Thus, there is a strong motivation and need to produce more and more diverse plants for food and less for feed. All this creates new demands and challenges for plant breeding that need to be addressed also by making use of emerging crop breeding techniques (Bilichak et al., 2020; Liu et al., 2021).

2 | PLANT PROTEINS FOR FOOD

2.1 | Protein yield and underutilised protein crops

Europe is dependent on the import of protein crops as grain legumes, both for animal feed and human food production (European Commission, 2018; Thierry et al., 2019). Breeding programmes for traditional crops as well as the use of underutilised or new crop species (see examples below) could help to increase plant-based protein production. In wheat (*Triticum aestivum*), with a grain protein content between 5% and 23% (Bogard et al., 2013; Tabbita et al., 2017), breeding and agronomic programmes to increase protein content without impairing yield have been prioritised for 20 years (Cohan et al., 2019; Cormier et al., 2016), reflecting the needs of the bread industry. Increasing the protein content is challenging because of a commonly observed negative correlation with grain yield (Monaghan et al., 2001), and the identification of cultivars deviating from this correlation is achieved via several breeding programmes (Bogard et al., 2013; Oury & Godin, 2007). The limitation for many cereals including wheat and rice is not necessarily nitrogen availability for protein synthesis but rather the mobilisation of existing protein reserves in the leaves and stem of the plants. The NAC transcription factor encoding genes *NAM-A1* and *NAM-B1* have been identified to be important in this context, that is to combine high protein content and high yield. The functional *NAM-B1* allele accelerates wheat

senescence and increases nitrogen remobilisation from the leaves to the grains (Uauy, 2006; Uauy et al., 2006; Waters et al., 2009), but it is rarely present in modern cultivars (Hagenblad et al., 2012; Tabbita et al., 2017). Protocols and recommendations for NAM-B1 introgression through marker-assisted selection have been made publicly available at <https://maswheat.ucdavis.edu/protocols/HGPC/index.htm> and facilitated the introgression of the functional NAM-B1 allele in different genetic backgrounds (Brevis & Dubcovsky, 2010; Kumar et al., 2011). So far, this allele has been used to produce 18 new commercial varieties (Tabbita et al., 2017). The homologous *NAM-A1* gene has a similar function (Avni et al., 2014), and its functional *NAM-A1a* allele is more widespread than *NAM-B1* in elite wheat germplasm (Cormier et al., 2015). The effect of *NAM-A1* is dependent on the environment (Cormier et al., 2015). In Australia, in conditions that favour short grain filling periods without heat and water stress, the *NAM-A1a* allele was linked to higher yield (Alhabbar et al., 2018). It appears clearly that the use of the *NAM-A1a* allele in elite material could be a real opportunity for improving grain protein concentration without reducing grain yield considering the local specificities of the senescence period and its sensitivity to late stresses (abiotic and biotic). Further sources of genetic variation to maintain high quality and yield should be sought. While protein level is perhaps the most immediate issue, the protein composition, for example the level of glutenin and gliadin, will also require attention for wheat flour quality, for example for the plasticity and elasticity of bread dough.

Regarding yield, the most important global source of plant proteins is soybean (*Glycine max*) with 2.77 t grain/ha in 2015–2019 (FAO, n.d.-b). The mature seeds not only have a protein content of c. 37% (USDA, 2019a) but also provide sufficient quantities of all essential amino acids (Hughes et al., 2011). However, additional efforts are needed to identify and improve varieties suitable for colder, long-day conditions (Kurasch et al., 2017).

Among the other cultivated legumes, faba bean (*Vicia faba* L.) has, after soybean, the highest yield worldwide (2.02 t grain/ha in 2015–2019) (FAO, n.d.-b) and produces seeds with a protein content of c. 26% (USDA, 2019b). In addition, faba bean is well adapted to cool climates such as Northern European summers and Southern European winters, where soybean does not perform well (Stoddard, 2017). One major obstacle to the wider adoption of faba bean, however, is the accumulation of the pyrimidine glucosides vicine and convicine that can cause haemolytic anaemia ('favism') in individuals deficient in glucose-6-phosphate dehydrogenase, which affects 5% of the world population (Luzzatto & Arese, 2018). A single genetic source of low vicine and convicine levels in faba bean has been identified (Duc et al., 1989), and the trait has been

bred into a handful of cultivars (Khazaei et al., 2019). Notably, the low-vicine trait does not appear to be linked to altered levels of protein, minerals or B vitamins (Khazaei & Vandenberg, 2020; Marshall et al., 2021). Recent efforts to uncover the causal mutation have resulted in the identification of *VC1*, a gene that encodes an enzyme normally involved in riboflavin biosynthesis and found to be inactivated in low vicine and convicine lines (Björnsdotter et al., 2021). Apart from providing a new hypothesis on the biosynthetic origin of vicine and convicine, likely from the riboflavin pathway, this work can serve as the foundation for the development of faba bean cultivars that are completely free of these substances.

Regarding new and underutilised legume crops, lupins (*Lupinus* spp.) are of special interest as their seeds can accumulate exceptionally high protein levels (up to 44%). There are four cultivated lupin species: narrow-leafed (*L. angustifolius*), white (*L. albus*), yellow (*L. luteus*) and Andean lupin (*L. mutabilis*). All of these need to be further optimised for yield stability, stress resistance, seed quality and early maturity (Abraham et al., 2019). With respect to seed quality, lupins accumulate toxic alkaloids in most tissue types, including seeds. Breeders have produced varieties impaired in alkaloid production ('sweet' varieties), but these are more susceptible to herbivores and can still surpass the safety threshold values for seed alkaloid content depending on seasonal variation. Interestingly, the lupin alkaloids are not produced in the seeds but transported to them from other plant parts (Otterbach et al., 2019). This gives opportunities for transport engineering as a way to block the transport of toxic alkaloids to the seeds, thereby producing a stable, non-toxic protein source (Otterbach et al., 2019). It is proposed that recent advances in lupin genomics could greatly facilitate corresponding breeding approaches (Hane et al., 2017; Hufnagel et al., 2020; Książkiewicz et al., 2017).

Over the past decades, quinoa (*Chenopodium quinoa*) has become known as a relevant protein crop outside of South America. Its seeds contain up to 19% protein, and, more importantly, quinoa provides all essential amino acids in sufficient quantities (Angeli et al., 2020). In rapeseed (*Brassica napus*)—the world's third largest oilseed crop and the largest in the EU (>17 mill tons seed, 2019) (USDA, 2021)—the seed contains approximately 40% oil and approximately 20%–35% protein (Wanasundara, 2011). The major storage proteins in the seeds are cruciferin (11S globulin) and napin (2S albumin) (Wanasundara, 2011). Rapeseed seeds have a well-balanced amino acid composition and thus are a potentially attractive protein source. Currently, rapeseed is grown for oil, and the protein is used in feed but only in reduced amounts due to the presence of antinutrients (see *Removing antinutrients, toxic metabolites, and heavy metals*) (Nega & Woldes,

2018). Despite much breeding efforts, the seed meal of the canola quality rapeseed varieties is not suited for human consumption due to the residual amount of glucosinolates and astringent bitter compounds (Hald et al., 2019). The intensive breeding efforts to improve oil content and to reduce glucosinolate levels of rapeseeds have concomitantly induced a decrease in the total protein content (Malabat et al., 2003). There is therefore potential to improve rapeseed as protein crop for human nutrition. Other alternative protein sources could be protein-rich seaweeds such as *Palmaria palmata* and *Porphyra* species, with a dry matter composition of 10%–30% protein (Kim, 2012), as well as microalgae like *Chlorella* species with up to 50%–60% protein content of dry matter (Safi et al., 2014).

2.2 | Protein functionality and plant storage proteins

For human nutrition, the most important plant protein sources are cereals and food legumes, including oilseed legumes. The grains of these species can be consumed without any protein purification (e.g. as flours) or after protein enrichment. In some cases, the enriched protein fraction is a co-product of oil or starch production (e.g. soy protein and gluten).

There are several reasons why plant proteins are still underutilised in human diet: (i) lower nutritional values (on a single source basis) as compared with animal proteins in regard of the amino acid composition, digestibility and the antinutrient content; (ii) difficulties, in the case of cereal proteins, in maximising their physical functionality due to their large molecular weight and size, and poor solubility in water; (iii) the economic cost associated with isolation and recovery of protein fractions (Day, 2013); and (iv) organoleptic limitations when compared to animal products. With respect to the latter, many plant-based foods lack sweetness and umami flavours interlinked with consumer acceptance and related to psychological, social and cultural elements (Schmidt & Mouritsen, 2020).

Plant storage proteins can be categorised into four major classes based on their solubility and extractability in various solvents (the ‘Osborne fractions’) (Osborne, 1924): albumins, globulins, prolamins and glutelins. Albumins contribute significantly to the total sulphur content (>50%) in the seeds of leguminous plants, even though they represent only 10%–30% of total proteins. Globulins are the major protein fraction in legumes seeds but are usually less abundant in cereal grains and contain relatively low sulphur levels. Based on their sedimentation coefficients, globulins are, in for instance pea (*Pisum sativum*), subdivided into 7S vicilins and 11S legumins. Prolamins are rich in proline and glutamine and are the

major storage proteins in cereals, accounting for about 50% of the total grain proteins, only in rice (*Oryza sativa*) they are minor components. Glutelins are also mainly found in cereal grains. Interestingly, a certain degree of homology at the primary sequence level has been shown between rice glutelins and the subunits of the 11S globulins in legumes (Zhao et al., 1983).

Accordingly, seed storage proteins are a mixture of different types of proteins. Pea seeds, for example, contain both albumin and globulin types. To add to the complexity, the recent pea genome revealed 12, 9 and 2 genes encoding the globulins legumin, vicilin and convicilin, respectively, and 8 and 9 genes encoding the PA1 and PA2 albumins respectively (Kreplak et al., 2019). The various globulin and albumin isoforms in pea vary in quantity in response to the environment (Bourgeois et al., 2009). The diversity is further magnified by the range of sites controlling pre-polypeptide cleavage and transcriptional regulatory regions that are presumed to modulate the accumulation of the storage proteins in response to developmental and environmental cues (Kreplak et al., 2019). The genetic variability provides the basis for selection of desired protein compositions.

2.3 | Biofunctionality: amino acid composition and digestibility

Proteins have two main complementary functions in food: bio- and technofunctionality. Biofunctionality is related to the proteins’ nutritional and physiological properties, while technofunctionality is related to physico-chemical properties affecting the appearance, texture and stability of food products (Day, 2013).

Plant proteins are often considered as incomplete or nutritionally inferior compared to animal proteins. This is likely due to lower availability and associated reduced overall digestibility of plant proteins and, in addition, a limited presence of some of the essential amino acids. However, in principle, there is no reason why plant proteins should not supply high quality protein and there are different approaches for doing so. Indeed, there are some crops like soybean and quinoa that provide all nine essential amino acids (Hughes et al., 2011; López et al., 2018). Histidine, leucine, isoleucine, lysine, methionine, phenylalanine, threonine, tryptophan and valine cannot be synthesised by humans and must be provided via the diet (Sá et al., 2020). The branched-chain amino acids leucine, isoleucine and valine are particularly important for promoting muscle protein synthesis. In general, cereals usually contain low levels of lysine, while legumes have a deficiency in the sulphur-containing amino acids methionine and cysteine (Sá et al., 2020). As an example,

the nutritional value of pea seed proteins decreases as the proportion of globulins, especially the 7S vicilin, increases because of their low sulphur amino acid content. Thus, the protein quality of the diet is significantly improved when a combination of proteins from cereals and legumes (Davies & Jakeman, 2020) is used, as it is done in a large number of traditional dishes. To optimise individual crops, further breeding efforts are needed to improve the amino acid composition of the major seed storage proteins. It was possible to breed high lysine varieties of some cereals, especially Quality Protein Maize (QPM) maize (*Zea mays*) varieties, whereas there has not been much progress yet producing high methionine/cysteine legumes. Likewise, there have been approaches to improve cereals by using genetic engineering, both by modifying amino acid metabolism and by adding different storage proteins. A combination of altering amino acid metabolism and storage protein composition appears especially promising to channel the amino acids into proteins (Azevedo & Arruda, 2010; Davies & Jakeman, 2020; Galili & Amir, 2013; Hagan et al., 2003; Kumar et al., 2020). A fortified staple crop containing sufficient quantities of all essential amino acids could be especially advantageous for the very poor, who cannot afford balanced diets based on several crops (Goredema-Matongera et al., 2021).

Protein digestibility is a measure of the susceptibility of a protein to proteolysis and depends on the protein structure, processing and the presence of antinutritional factors (see *Removing antinutrients, toxic metabolites and heavy metals*). Solubility and especially the structure of the globulins influence proteolysis. It is well-established that nutritional and technological properties of plant storage proteins can largely vary according to their secondary structure (Gabriel et al., 2008; Rubio et al., 2014).

2.4 | Technofunctionality

The technofunctionality of plant proteins in food, for example solubility, viscosity, foaming, emulsifying and gelling ability as well as fat absorption capacity, is determined by the types of proteins in the seed. The functional properties of pea proteins for food are, for instance, to some extent determined by the vicilin (7S) and legumin (11S) content. This is related to their inherently stable native protein structure. Consequently, these globulins are relatively thermostable and appear to unfold only partially with minor conformational changes during common food processing (Day, 2013; Grossmann & Weiss, 2021; Sui et al., 2021).

It seems that the 7S seed proteins of soybean and pea (beta-conglycinin and vicilin respectively) have better emulsifying properties compared with the 11S glycinin/

legumin type proteins. This is probably due to smaller molecular mass, higher structural flexibility, the presence of glycosylated groups and higher hydrophobicity (Keerati-u-rai & Corredig, 2010). This is further supported by studies in pea where the ratio of legumin and vicilin can vary from 0.4 to 2.0 depending on the cultivar (Lam et al., 2018). Protein isolates from cultivars with a lower legumin/vicilin ratio showed better solubility, emulsifying capacity and stability, and foaming capacity and stability (Cui et al., 2020). For gelation, the 7S/11S ratio is also important as it influences gel fracture behaviour, firmness and/or elasticity. Gelation of 7S proteins is mainly based on hydrogen bonding and hydrophobic interactions with no covalent disulphide bonds, whereas gelation of 11S proteins involves disulphide crosslinks (Shomer et al., 1995). Interestingly, among legumes, common bean (*Phaseolus vulgaris*) seeds accumulate mostly 7S vicilin (about 50% of the total seed proteins) while 11S legumin is only a minor fraction (Vitale & Bollini, 1995). From a technological point of view, a comparative study between common bean and pea protein isolates indicated better gelation properties for common bean protein isolates (Shevkani et al., 2015). Thus, the ratio of 7S to 11S type proteins influences the technofunctionality of legume protein isolates and would be a relevant trait to target by breeding. The required ratio depends on the application, for example if a product similar to meat or dairy products is aimed for.

3 | MICRONUTRIENT QUALITY

Micronutrients, that is vitamins and minerals, are essential for human nutrition, and micronutrient deficiency is still a widespread problem, particularly in low- and middle-income countries (Bailey et al., 2015; WHO, 2019). Fortification of processed food is one option to improve nutritional quality (Olson et al., 2021). Biofortification aims to directly increase the micronutrient content of edible plant parts, and this approach could, especially in the case of staple foods, provide a healthier diet to the rural poor, which are most threatened by micronutrient deficiencies (Foley et al., 2021; Hotz & McClafferty, 2007). Biofortification has been achieved via transgenic and conventional breeding approaches. Examples of transgenic approaches include folate (vitamin B9) production in rice, which has been genetically modified to increase folate content up to 150-fold by overexpressing genes encoding *Arabidopsis thaliana* GTP-cyclohydrolase I (GTPCHI) and aminodeoxychorismate synthase (ADCS) (Blancquaert et al., 2015). Similar approaches were used to increase the level of provitamin A (β -carotene) in rice (Paine et al., 2005; Ye et al., 2000), rapeseed, flax (*Linum usitatissimum*), potato (*Solanum tuberosum*), tomato (*Solanum*

lycopersicum), maize, soybean and wheat (Jiang et al., 2017). Vitamin C (ascorbate) contents were increased in lettuce (*Lactuca sativa*) and tomato by either overexpressing genes of the biosynthesis pathway or silencing genes involved in ascorbate recycling (Gest et al., 2013; Jain & Nessler, 2000). Vitamin E (tocopherol and tocotrienol) contents were increased in rapeseed, lettuce, soybean and tomato by overexpression of individual genes or the whole biosynthetic pathway (Jiang et al., 2017; Lu et al., 2013). To increase the level of multiple vitamins in maize, several of these approaches were combined (Naqvi et al., 2009). Biofortified crops developed using conventional plant breeding approaches include provitamin A-rich orange sweet potato (*Ipomoea batatas*), orange maize and yellow cassava (*Manihot esculenta*) (Laurie et al., 2012; Pixley et al., 2013; Ugochukwu Onyeneke et al., 2019). Alternatively, biofortification could be achieved through induced conversion of a plant organelle into a storage organelle, for example the conversion of chloroplasts into chromoplasts storing provitamin A (Llorente et al., 2020). A special case is vitamin B₁₂ (cobalamin) that is only produced by bacteria. In contrast to all other vitamins, plants are thus not a source of this vitamin for human nutrition (Allen et al., 2018). Some algae acquire vitamin B₁₂ through a symbiosis with bacteria (Croft et al., 2005). Vitamin B₁₂ pathways have not yet been introduced into plants.

Recent efforts to enhance mineral contents in crops focus on iron and zinc. In rice, iron and zinc levels have been elevated by overexpressing the barley nicotianamine synthase HvNAS1 that acts as a chelator of metal cations such as Fe(II) and Zn(II) (Nozoye, 2018). In wheat, iron content has been improved by endosperm-targeted intragenic overexpression of a gene encoding ferritin TaFer1-A, resulting in a 50%–85% increase in iron content (Borg et al., 2012). A potential target for breeding to improve zinc content could be genes encoding the transcription factors bZIP19 and bZIP23 that both act as zinc sensors. Arabidopsis plants with mutated zinc-binding motifs accumulated two- to threefold more zinc in seeds (Lilay et al., 2021). This approach was not yet explored in crop species, in which also the largely Zn-specific effects have to be confirmed.

Whereas progress has been made regarding the mechanisms of mineral uptake from the soil, the knowledge about the distribution in the plant and how minerals accumulate in the seeds is still limited. The variability in zinc and iron content—constituting a fourfold difference between aromatic lines and popular cultivars of rice and a threefold difference between different wheat cultivars—could provide the genetic base for improvements of elite germplasm. In some regions of the world with poor soils, there may be substantial geospatial variability in

micronutrient grain composition (calcium, iron, selenium and zinc) at subnational scales due to soil, environment, and crop type (Gashu et al., 2021). Biofortification may need to account for such geographical effects.

4 | HEALTH-PROMOTING SPECIALISED METABOLITES

Health-promoting specialised metabolites are of interest in the context of improving nutritional quality. Dietary polyphenols, for instance, have antioxidant, anti-inflammatory and anti-diabetic effects (Belwal et al., 2017; Miguel, 2011). Polyphenols include different classes of compounds, among which are flavonoids, phenolic acids, stilbenes and anthocyanins. Metabolic engineering approaches in crops and horticultural species have been successfully used mainly by acting on polyphenol regulatory and structural genes to redirect the metabolic fluxes. For example, MYB and bHLH transcription factors have been reported to modulate flavonoid and anthocyanin production in different species (Scarano, Chieppa, et al., 2018). In tomato, the expression of the transcription factors AmRosea1 (MYB) and AmDelila (bHLH) from snapdragon (*Antirrhinum majus*) improved the synthesis of anthocyanins in fruits (Butelli et al., 2008). Furthermore, the overexpression of a stilbene synthase gene from grape (*Vitis vinifera*) in tomato was able to redirect the metabolic flux and resulted in the synthesis and accumulation of stilbenes, such as resveratrol, a phytochemical prized for its antioxidant benefits (Salehi et al., 2018). Subsequently, a multilevel approach of metabolic engineering was recently applied to enrich crops in different classes of dietary polyphenols and therefore to further improve their nutritional quality. Combining the metabolic engineering for flavonoids, anthocyanins and stilbenes generated a new tomato line named ‘Bronze’, referring to the colour of the fruit skin, which accumulated high levels of these polyphenols, thus providing a higher global polyphenol content and higher antioxidant/anti-inflammatory properties to the whole fruit (Scarano, Butelli, et al., 2018).

5 | HEALTH-PROMOTING LONG-CHAIN POLYUNSATURATED FATTY ACIDS

In recent years, metabolic engineering approaches have been successfully used to produce essential fatty acids in oilseeds. Plant seeds have been developed as a platform for the design and tailoring of biochemical pathways to synthesise diverse nutritional and industrial oils not currently found in oilseed crops (Haslam et al., 2016). The

omega-3 (n-3) long-chain polyunsaturated fatty acids (LC-PUFA), eicosapentaenoic acid (EPA; 20:5 n-3) and docosahexaenoic acid (DHA; 22:6 n-3) are essential components of a balanced human diet. LC-PUFAs play a vital role in neonatal and infant development (childhood stunting) as well as cardiovascular health (CVD) and metabolic pathologies such as type-2 diabetes. Humans have a limited capacity to synthesise these omega-3 LC-PUFAs; therefore, the importance of identifying new sources of LC-PUFA should not be underestimated (Calder, 2018). EPA and DHA are found to be predominantly enriched in wild and farmed fish consuming these fatty acids as part of their diet. Increasing demand and specialised dietary preferences, however, make this an unsustainable long-term production method. Seaweeds (van Ginneken et al., 2011) and microalgae (Wells et al., 2017) are another source for LC-PUFAs. In contrast, several crop plants produce many different types of fatty acids, but none produces EPA or DHA. A promising platform for specialised oil production is *Camelina sativa*, an oilseed crop of the Brassicaceae family, due to its hardiness, short cropping cycle and disease resistance. Using a transgenic approach, genes coding for proteins necessary for EPA and DHA synthesis from marine microorganisms have been introduced into camelina, showing that this crop is suitable for effective omega-3 LC-PUFAs production (Usher et al., 2017). Genetically modified EPA and DHA enriched camelina can serve as a food source for farmed fish as well as a direct dietary nutritional supplement for human consumption. Other examples of oil production using camelina are acetyl glycerides, hydroxylated fatty acids, medium-chain fatty acids, ω -3 long-chain polyunsaturated fatty acids, palmitoleic acid (ω -7) and other high-value oils (Yuan & Li, 2020).

6 | ANTINUTRIENTS, TOXIC METABOLITES AND HEAVY METALS

Antinutrients, primarily produced as defence compounds, can adversely affect biological functions when being consumed. Examples are phytate, oxalate, glucosinolates, raffinose family oligosaccharides and tannins. Accordingly, to substantially improve crop nutrient quality, a targeted engineering approach is needed to reduce antinutrient concentrations in edible plant parts. For instance, mutations in several transporters have been shown to reduce glucosinolate levels in the seeds of different brassica species (Nour-Eldin et al., 2017). The accumulation of phytate (myo-inositol hexakisphosphate), a strong mineral chelator that is the main constrain for iron and zinc bioavailability in humans and phosphorous in monogastric animals, has been reduced through identification of

low phytic acid (*lpa*) mutants in barley (*Hordeum vulgare*), common bean, maize, rice, soybean and wheat. However, these mutants often have negative pleiotropic effects including reduced tolerance to abiotic stress, reduced germination and stunted growth (Meis et al., 2003; Pilu et al., 2005; Stevenson-Paulik et al., 2005; Tong et al., 2017). These negative effects could potentially be compensated through breeding.

Besides metabolites, there are also proteins with antinutrient activity such as lectins, protease inhibitors and α -amylase inhibitors. They are particularly abundant in the seeds of legumes. These proteinaceous antinutritional factors are thermolabile and therefore not of concern in processed (cooked) food for humans. However, for the production of feed, there are incentives to reduce or abolish the accumulation of such proteins, including screening approaches to identify mutants devoid of these proteins in soybean (Schmidt et al., 2015), common bean (Sparvoli et al., 2016) and pea (Clemente et al., 2015).

In addition to antinutrients, toxic metabolites such as cyanogenic glycosides, saponins or quinolizidine alkaloids can prevent the use of otherwise suitable plants as food and feed. In cassava, cyanogenic glycosides have been reduced by either targeting their biosynthesis (Jørgensen et al., 2005) or by increasing their degradation (Narayanan et al., 2011). Low saponin (sweet) varieties of quinoa have been described (Melini & Melini, 2021), but their genetic base is not yet uncovered. Besides targeting genes regulating alkaloid production or degradation in lupins (Hufnagel et al., 2020; Yang et al., 2017), the accumulation of alkaloids in seeds could be avoided by reducing their transport into seeds (Otterbach et al., 2019).

Besides plant-produced antinutrients and toxic metabolites, heavy metals accumulating in crops can be a health burden. For instance, food intake is responsible for a large fraction of cadmium (Cd) exposure, and natural variation could be exploited in breeding programmes to reduce Cd accumulation in edible plant organs (Clemens et al., 2013; Maccaferri et al., 2019).

7 | CONCLUSION

A more plant-based diet is both healthier and more sustainable. However, crop composition in terms of nutrient diversity and quality of individual crop species needs to be optimised (Figure 1). In some cases, desired combinations of characteristics can be achieved, for example wheat varieties with a functional *NAM-B1* allele were shown to have a higher protein content and increased levels of the micronutrients iron and zinc (Tabbita et al., 2017). Other nutritional qualities seem mutually exclusive, for example wheat varieties with high protein levels seem to have a

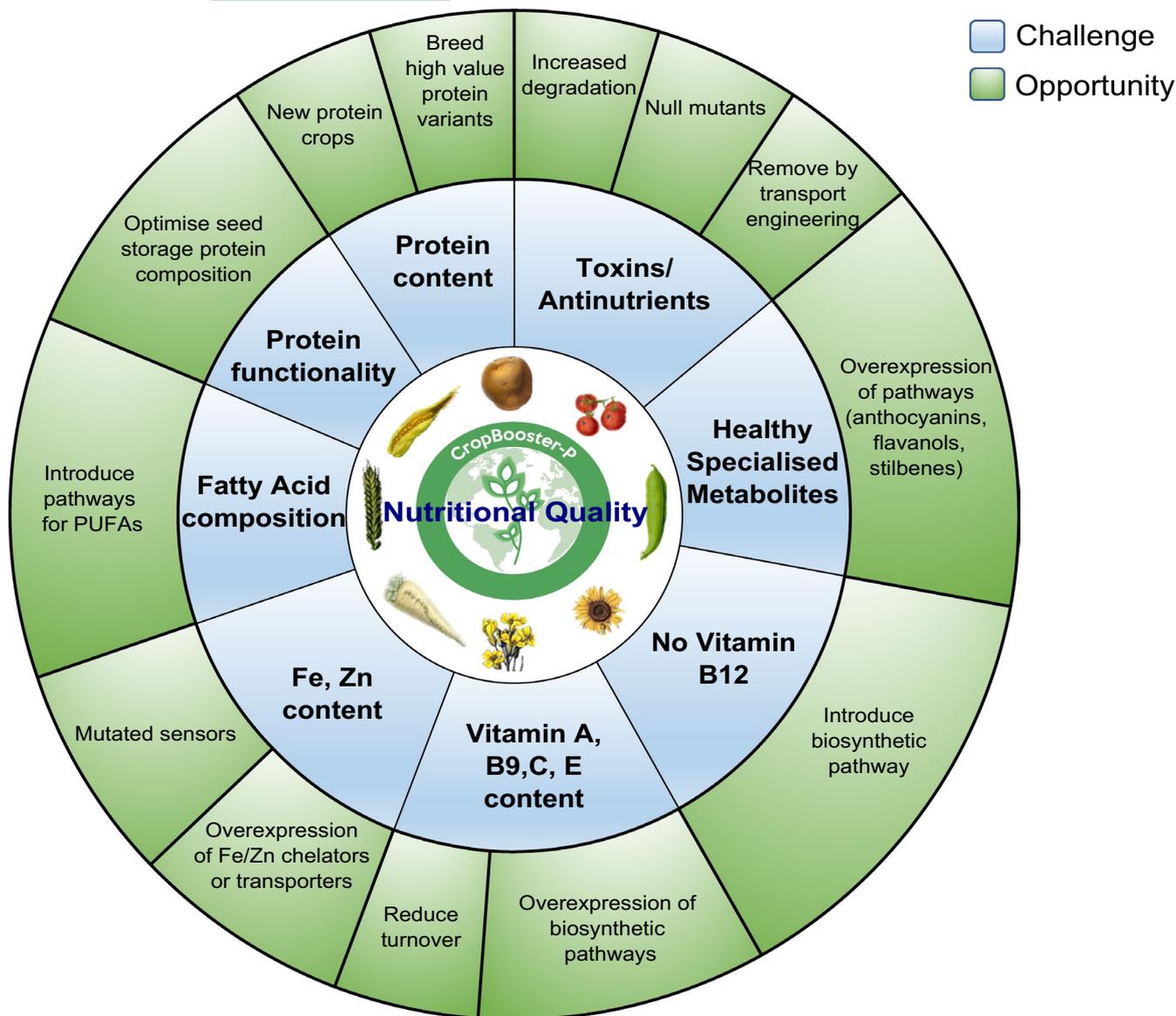


FIGURE 1 Prospects to improve the nutritional quality of crops including challenges (blue) and opportunities (green). PUFA = long-chain polyunsaturated fatty acids; Fe = iron; Zn = zinc; (pro)vitamin A = β -carotene; vitamin B9 = folate; vitamin B12 = cobalamin; vitamin C = ascorbate; vitamin E = tocopherol and tocotrienol. Certain indicated challenges can be correlated: for example high protein content can be linked to high iron and zinc content (positive correlation) or an increase in minerals needed as micronutrients can be followed by an increase in detrimental heavy metals (negative correlation)

lower starch content or rapeseed varieties with high oil content usually have lower protein content. Also, desirable characteristics could cause unwanted side effects, which would need to be thoroughly investigated, for example increasing the mineral content for micronutrient improvement might lead to a sequential accumulation of toxic heavy metals. Further, accelerated conventional and molecular breeding efforts will be required to improve and use versatile and diverse plant sources, including so far underutilised crops. Moreover, crops can be specifically engineered to be more suitable for the production of specific types of food in regard to their macro- and micronutrient content as well as specialised metabolite

composition. The progress of these breeding and engineering approaches, particularly regarding underutilised crops, depends on available resources such as the identification of trait-related alleles, genomic sequences, functional transformation and regeneration protocols, and the implementation of advanced breeding methods such as genome-wide association (GWA) approaches (Biazzi et al., 2017) and CRISPR/Cas based technologies (Zhang et al., 2020).

To meet the future global needs, it will also be crucial that the approaches to improve nutritional quality are complemented by advances to increase plant yield while promoting sustainability. These reviews are based

on a database (LINK: <https://www.cropbooster-p.eu/the-project/project-results.html> or <https://drive.google.com/open?id=18x-oJv8vUrgXs8Jkf7IbouP1WkriYixK>) established in the framework of the CropBooster-P project.

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