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REVIEW

Drought and heat affect common bean minerals and human diet—What we know and where to go

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Abstract

Global climate change, causing large parts of the world to become drier with longer drought periods, severely affects production of common beans (*Phaseolus vulgaris* L.). The bean is worldwide the most produced and consumed food grain legume in the human diet. In common beans, adapted to moderate climates, exposure to drought/heat stress not only results in significant reduction of bean yield but also the nutritional value. This review explores the contribution of common beans to food and nutrient security as well as health. Also discussed is the existing knowledge of the impact of drought/heat stress, associated with a changing climate, specifically on iron (Fe) and phytic acid (PA) that are both among the most important mineral and anti-nutritional compounds found in common beans. Further discussed is how the application of modern "omics" tools contributes in common beans to higher drought/heat tolerance as well as to higher Fe and reduced PA content. Finally, possible future actions are discussed to develop new common bean varieties with both improved drought/heat tolerance and higher mineral (Fe) content.

KEYWORDS

antinutrients, biofortification, climate change, common bean, drought/heat, legumes, minerals, *Phaseolus vulgaris*, phytic acid, pulses

1 | INTRODUCTION

1.1 | Climate change and crop production

Global climate change will severely affect the UN goal to sustainably produce enough food by 2050 to feed a projected global population of 9.1 billion people. This is despite previous progress in addressing global undernutrition with increased food production by agricultural expansion and intensification (Myers et al., 2017). Global climate change, which has a long-term impact in the form of different abiotic stresses (Redden, 2013), will particularly cause large parts of the world to become drier with longer drought periods, more intense heat and irregular rainfall. These changes will severely affect agriculture as well as the stability and distribution of food production (Kellogg & Schware, 2019). These changes in the climatic conditions might even become progressively worse (Hao et al., 2018). A major factor in driving such temperature increase and altering precipitation patterns is a higher atmospheric carbon dioxide (CO_2) concentration (Kellogg & Schware, 2019; Lindsey, 2020).

Warmer and drier climatic conditions, resulting in increased evaporative losses, will also drive the demand for more water. A substantial part of the world's agriculture is, however, already suffering from chronic soil water shortages due to severe drought conditions (Nadeem et al., 2019). Predicted shifts in crop production, due to regional changes in temperature and rainfall patterns, might further worsen local food shortages. The future demand for affordable nutritious food will, therefore, require integration of such regional predictions within drought monitoring and forecasting (Leisner, 2020; Mbiriri et al., 2018; Myers et al., 2017; Parsons et al., 2019; Zolina et al., 2013).

1.2 | Drought/heat stress and plant growth

Stresses associated with a changing climate are predicted to severely impact plant metabolism as well as soil fertility and carbon sequestration. This impact will limit plant growth and productivity and, ultimately, availability of nutritious food (Dankher & Foyer, 2018; Myers et al., 2017). A higher atmospheric CO_2 concentration affects, for example, the nutritional composition of crops by reducing the protein content of the edible plant parts and also lowering concentrations of important minerals (Loladze, 2014; Medek et al., 2017; Myers et al., 2014). In particular, soil water deficit, due to drought/heat conditions, causes considerable reduction in plant productivity. This reduction is specifically evident in areas where the agricultural system is dependent on rainfall, such as on the Southern Plains of the USA and in eastern Africa (Adhikari et al., 2015; Ahmed & Stepp, 2016; Steiner et al., 2018). Impacts of drought/heat range from negatively affecting all plant development stages with key physiological, biochemical and metabolic pathways seriously disrupted (Dankher & Foyer, 2018). Temperature extremes are further more strongly associated with a reduction in crop yield, compared to precipitation extremes, and irrigation partly limits the negative effects of high temperatures (Vogel et al., 2019). While plants are always exposed to a combination of stresses under field conditions (Hussain et al., 2018), most studies have focused on the impact of individual stresses on crop yield (Fahad et al., 2017). Combined drought and high temperature stress is known to reduce yields of maize, soybean and wheat (Matiu et al., 2017). Physiological characterization of plants exposed to either drought or heat stress, or a combination of both stresses, has indicated that combined stresses have several distinctive characteristics. These characteristics include low photosynthesis combined with increased respiration and closed stomata combined with increased leaf temperature (Mittler, 2006). However, how plants respond to a combination of different abiotic stresses cannot be simply inferred by the response of the plant to an individual stress (Mittler, 2006). To develop strategies maintaining crop productivity under such individual or combined stresses is, therefore, a major future research challenge (Ferguson, 2019).

1.3 | Potential of legumes

Legumes, as members of the large Fabaceae (Leguminosae) family, are predominantly grown in the world's tropical and subtropical areas. The production and consumption of pulses, the edible seeds of legumes, has further greatly increased over the last 15 years (Rawal & Navarro, 2019). Legumes include a number of important agricultural and food plants, such as Glycine max (soybean) and Phaseolus species (beans). They have an important function in both the diversification and sustainable intensification of agriculture. Apart from being a major dietary protein source, legumes are a rich source of minerals to humans and animals. Stresses, associated with changing climatic conditions, pose, however, a severe threat towards their growth, yield potential as well as nutritional value (Foyer et al., 2016; Gepts et al., 2008; Latef & Ahmad, 2015; Nadeem et al., 2019; Sica et al., 2021; Vasconcelos et al., 2020). An important feature of legumes is further the ability to form root nodules allowing to fix atmospheric nitrogen. With the help of rhizobia, legumes reduce atmospheric nitrogen to ammonia in these root nodules with various genes required for symbiotic nitrogen fixation (SNF) (Roy et al., 2020). The natural ability to add fixed nitrogen into soils renders legumes a keystone species for natural and agricultural ecosystems, injecting over 50 million tons of nitrogen into the soil per annum (Roy et al., 2020). SNF, which significantly contributes not only to protein production but also to increase in soil fertility (Sørensen & Sessitsch, 2007; Wagner, 2011), is, however, highly drought sensitive (Kunert et al., 2016).

1.4 | Common beans and abiotic stress

Among the legumes, common bean (*Phaseolus vulgaris* L.; Figure 1), which is the focus of this review, is the most produced and consumed food grain legume worldwide. Common beans are adapted to relatively moderate climatic conditions and not to extreme climatic and edaphic environments. Day temperature exceeding 30°C or night temperatures higher than 20°C can significantly reduce seed yield due to flower abscission, development of parthenocarpic pods (pin pods), lower seed set per pod as well as decreased seed size (Rainey & Griffiths, 2005). Soil degradation and factors, such as soil acidy and aluminium toxicity, lead to deficiencies in nitrogen and phosphorus. This can limit root development and consequently access to soil moisture (Samago et al., 2018).

Growth of legumes is generally affected by several abiotic stresses causing as a response changes in the plant phenotype (Araújo et al., 2015). Among the reported changes in common beans due to abiotic stresses are less leaf expansion due to ultraviolet-B radiation (Riquelme et al., 2007), increase of production of malondialdehyde, antioxidants and carotenoids, a decrease in the chlorophyll content of leaves due to heavy metal exposure (Zengin, 2013), reduction of seedling emergence after low temperature treatment (De Ron et al., 2016), as well as suppression of growth, photosynthesis and transpiration under high soil salinity (Kaymakanova et al., 2008). Changes in protein expression, reduced germination, stunted growth, serious damage to photosynthesis and a reduction in nutrient uptake particularly occur after exposure to drought/heat stress, (Mathobo et al., 2017; Nadeem et al., 2019; Zadražnik et al., 2013). In addition, a shallow root system further renders common beans vulnerable to any shortage of soil water with the reproductive stage, which includes flowering and pod-filling, also very drought-sensitive (Daryanto et al., 2017).

Adaptation, particularly to drought conditions, includes the improvement in the photosynthetic capacity, water-use efficiency and adaptation to different environments. Such adaptation has been already found in a few common bean genotypes, including the BAT477 race (Beebe et al., 2008; Polania, Rao, et al., 2016), and selection for drought resistance improved yield in phosphorus limited environments (Beebe et al., 2008). Root traits for improved water uptake include existence of more small fine roots, higher root length as well as higher root density (Fenta et al., 2020; Polania et al., 2017). In drought-tolerant common beans, maturity acceleration with a high seed filling rate further limits any drought impact (Rosales-Serna et al., 2004). Besides improved remobilization and partitioning of photosynthates (Teran et al., 2019), a change of canopy biomass and harvest index has also been found to contribute in common beans to more drought tolerance (Assefa et al., 2015; Polania, Rao, et al., 2016). Hageman et al. (2020) further provided evidence that resource partitioning from pod walls into seeds and the inherent sensitivity of leaflet growth rate to drought can be used as further indicators for drought sensitivity/tolerance. When screening 25 common bean genotypes with contrasting drought tolerance in a phenotyping platform under different water supply conditions, gas exchange and osmotic adjustment together with increase in grain yield were also proposed as useful indicators for selecting more drought-tolerant common bean lines (Lanna et al., 2018). Polania et al. (2016) further reported that the best nitrogen-fixing common bean lines under soil water deficit are more drought-tolerant. But common bean genotypes, even more tolerant to soil water deficit, can ultimately be severely affected by nitrogen-deficiency under such soil water deficit (Beebe et al., 2014).

FIGURE 1 Common bean plants (left) and effect of drought on common beans (right) (adapted from Michigan State University Department of Plant, Soil and Microbial Sciences at https://www.canr.msu.edu/beanbreeding/research/drought)

Abiotic stresses further affect the nutritional quality of common beans (Sica et al., 2021). Variability in rainfall affects, for example, the production of secondary metabolites, such as phenolics. This change directly impacts the bean's health-related benefits and sensory qualities (Ahmed & Stepp, 2016). Mild drought stress increases certain phenolic compounds without affecting the seed yield (Herrera et al., 2019). Studies investigating irrigation effects further found that the total fibre decreases under rain-fed conditions. Water availability, however, also influences the digestibility of bean carbohydrates, extractable polyphenols and, depending on the bean variety, the antioxidant capacity (Ovando-Martínez et al., 2014). Only a few studies have so far investigated in greater detail the impact of stresses associated with climate change, such as drought/heat stress, on the bean's mineral and antinutrient content with phytic acid (PA) a potent antinutrient (Hummel et al., 2018).

The aim of this review is, therefore, to discuss the current existing knowledge on the link between drought/heat stress and content of Fe and PA in common beans. In our review, we will first provide a short general overview on the contribution of common beans to food/nutrient security as well as health. This will include the guidelines dictated by countries to improve human diet-related habits and lifestyle, and the role of antinutrients. We will then review the existing knowledge with regards to Fe and PA content in common beans and how drought/heat stress affects the content of these two compounds. Figure 2 provides a simplified overview of the processes specifically reviewed. A discussion will follow on how breeding using modern “omics” approaches has so far contributed not only to more drought/heat stress tolerance in common beans but also to identify genes involved in drought/heat stress tolerance as well as increase in Fe content and reduction in the PA content. Finally, we will discuss areas for possible future exploration of existing knowledge in common beans regarding increasing Fe and antinutrient content particularly under drought/heat stress conditions.

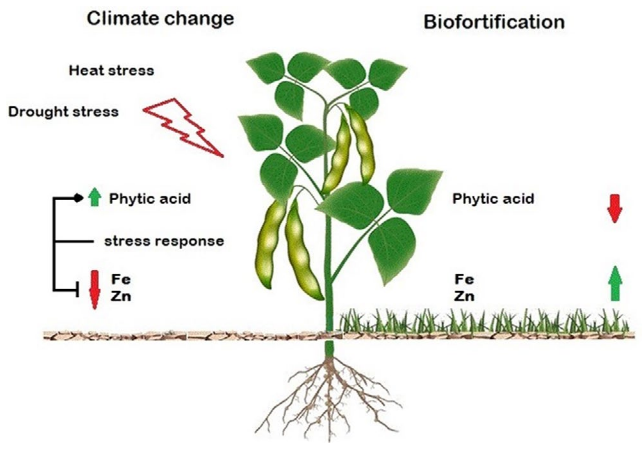

FIGURE 2 Effect of drought/heat stress on minerals and phytic acid in common beans and the consequences of biofortification

2 | FOOD AND NUTRIENT SECURITY

2.1 | Food security

Globally, common beans are grown on 23 million ha (http://www.cgiar.org/ our-research/crop-factsheets/beans) and the global common bean production has now risen to 12 million tons (mt) per year (FAO, 2014, 2018; Heinemann et al., 2016). The bean greatly contributes to overall food and nutrient security particularly in sub-Saharan Africa and in Central and Southern American countries (Beebe, 2012; Broughton et al., 2003). Latin America is the region with the greatest production of common beans, representing about 50% of world volume, followed by Africa with 25% (Figure 3). In sub-Saharan Africa, common beans are produced on more than 3.5 million ha with production taking place mainly in East Africa, the lakes region and the highlands of Southern Africa, with a combined production of almost 1 mt (Demelash, 2018). In Latin America, per capita annual consumption of common beans ranges from 10–18 kg, whereas in East Africa common annual bean consumption can be as high as 50 kg per capita.

In 2019, Myanmar, India and Brazil were further the top three dry bean producing countries in the world and Myanmar and India produced each over 5 mt (FAOSTAT, 2020; Table 1). In Latin America, Brazil was in 2019 the main producer of dry beans, with about 2.8 mt, followed by Mexico with about 0.9 mt. In Europe, only about 544,330 ha were cultivated with beans, with a production of about 1.9 mt (https://www.pulsesincrease.eu/crops/common-bean; accessed August 2021). Although having the lowest production area of all top dry bean producers, the United States of America (Table 1) achieved the highest bean yield in 2019 (1979 kg ha^{-1}). This was most likely due to a better technological input and also better seed quality. However, in India, despite having the greatest cultivation area, bean yield is still very low (418 kg ha^{-1}; Table 1). Such low yields in countries, such as India, Mexico and Kenya, are very likely due to a low technological input by resource poor farmers, irregularities of rainfall as well as poor seed quality.

Low input agricultural systems further account for the majority of common bean production and small-scale farmers particularly depend on beans for food and income (Kermah et al., 2017). They use, however, poor quality seed material caused by poor storage, seed-borne fungal infection as well as sowing and harvesting under unfavourable environmental conditions (Oshone et al., 2014).

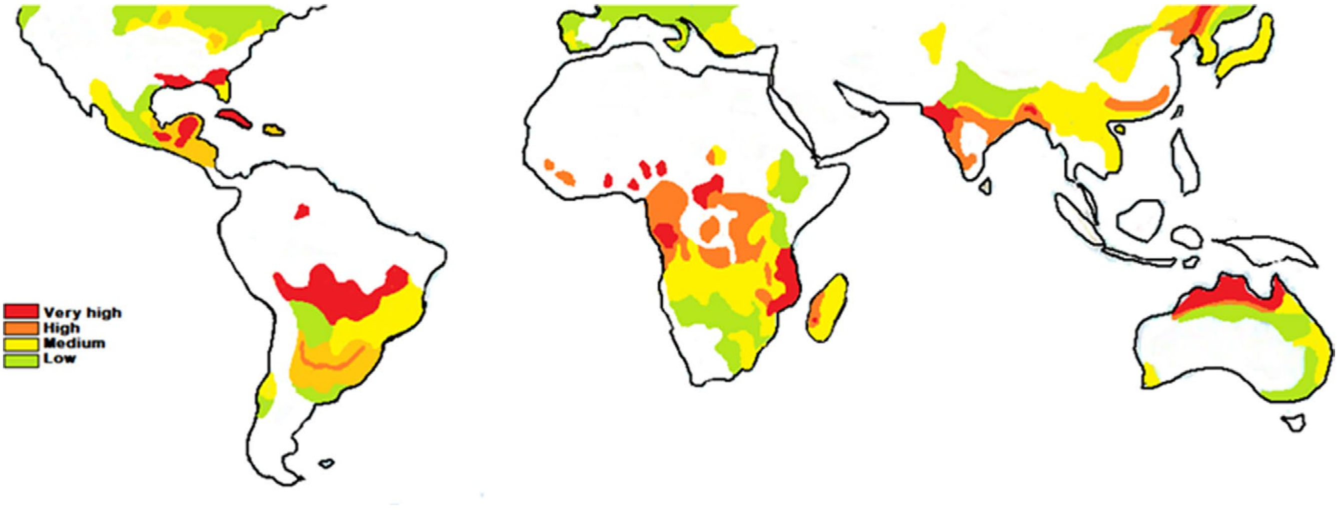

FIGURE 3 Impact of climate change on the suitability of bean production (adapted from Beebe et al., 2011). White areas represent areas where common beans are either not extensively grown or where climate change might have very little impact on bean growth

TABLE 1 Top common bean producing countries in the world

	Area (ha)	Production (kg/ha)	Total production (tons)
Myanmar	3.201.135	1826	5.845.272
India	12.690.696	418	5.309.787
Brazil	2.610.585	1113	2.897.749
China	745.936	1739	1.297.182
United Republic of Tanzania	893.570	1340	1.197.383
Uganda	539.660	1815	979.482
United States of America	470.890	1979	931.891
Mexico	1.207.395	728	878.983
Kenya	1.167.543	639	746.059

Note: Source: Food and Agriculture Organization Statistical Databases was used to develop this table; FAOSTAT, 2020).

They further grow beans in association, or in rotation, with maize with minimal production inputs (Rurangwa et al., 2018). Cereals are thereby grown on more fertile fields and legumes on soils depleted in nutrients (Chekanai et al., 2018; Kelly et al., 1998). Due to its existing SNF capacity, although lower when compared to soybean and faba beans (Peoples et al., 2009), common beans can grow on such marginal lands. Although common bean varieties with high SNF capacity and environmental resilience would be, therefore, of great benefit (Wilker, 2021), common bean breeding seldom includes selection for the SNF trait. In addition, modern bean production practices involve the application of nitrogen-fertilizer which causes not only SNF downregulation but also environmental pollution (Wilker et al., 2019). To solve this problem, moderate phosphorus fertilization in combination with an appropriate more affordable Rhizobium inoculation as a nitrogen source might be one potential option for improved production, especially under soil water deficit (Kibido et al., 2020; Samago et al., 2018). Overall, all these problems ultimately limit bean yields to low as ≤0.5 t ha^{-1}. This not only greatly affects smallholder systems (FAO, 2014; Rao et al., 2016), but prevents the realization of the bean's full yield potential and causes production instability from 1 year to the other. Most worrying, based on crop modelling, the majority of current common bean growing areas, especially in south-eastern Africa, will be in 2050 unsuitable for bean cultivation greatly affecting food and nutrient security (Hummel et al., 2018).

As much as one-third of bean production areas are further influenced by drought/heat stress. This greatly affects the contribution of common beans to food and nutrient security (Beebe et al., 2014; Kazai et al., 2019). Common bean production areas particularly subjected to frequent droughts are highland Mexico, the Pacific coast of Central America, northeast Brazil, and eastern and southern

Africa from Ethiopia to South Africa (Beebe et al., 2013). More than 60% of the world's common beans are cultivated under non-irrigated conditions in areas where seasonal rainfall is erratic and beans grow under rain-fed conditions (Seidel et al., 2016; Smith et al., 2019). Drought/heat stress can cause yield losses of up to 80% in these rain-fed production systems (Kazai et al., 2019), Specifically, intermittent or terminal drought stress causes severe yield loss (Beebe et al., 2013), although drought stress towards the end of the growing season might not cause much harm for grain yield (Mathobo et al., 2017). Irrigation would, therefore, allow to increase common bean production. Indeed, in Brazil yields of around 2900 kg ha^{-1} have been already obtained by irrigation (Alves Souza et al., 2020).

Recent modelling studies raise further concern for future food and nutrient security. They predict a significant decrease in the future suitability to grow common beans due to increased drought and also heat stress (Heinemann et al., 2017). In Africa, for example, where an estimated 682,000 ha of beans are currently cultivated, annual yield loss due to drought/heat conditions is already in the range of 781,000 t. Simulation models to characterize bean production in Brazil in rain-fed environments also indicate that climate change will cause more frequent but less severe drought conditions (Heinemann et al., 2017). A previous ecological diversity study with wild common bean accessions covering a habitat from Mexico to Argentina further found that accessions are distributed among different precipitation regimes following a latitudinal gradient. The habitat ecological diversity of the collection sites was further associated with natural sub-populations (Cortés et al., 2013). Finally, current common bean areas might also shift to colder regions of the Northern Hemisphere, such as Canada, the Nordic countries and Russia, as indicated by recent model projections (Ramirez-Cabral et al., 2016). How these changes will actually affect overall bean production has still to be investigated in more detail.

2.2 | Nutrient security

In contrast to the industrialized world, common bean is the most important grain legume consumed in areas with a low income where health is influenced mainly by dietary deficiencies rather than by excesses. Common beans are therefore also regarded, as other pulses, the “poor man's meat”. As a food staple, common beans contribute up to 35% of the protein and 340 calories/100 grams to the daily diet of resource poor urban and rural families. Food, however, not only needs to satisfy the caloric requirements, but has ultimately to provide sufficient amounts of nutrients such as minerals and vitamins (Muller et al., 2017). Common beans are an important source for the minerals Fe and Zn (Beebe et al., 2000; Castro-Guerrero et al., 2016; Drewnowski, 2010; Graham et al., 2007; Hall et al., 2017; Mitchell et al., 2009). For a general overview of the nutritional value of common beans, see https://feedtables.com/content/common-bean and also Celmeli et al. (2018). Fe and Zn deficiency further affects over 30% of the world's population (Bailey et al., 2015). Common bean has, therefore, the potential to not only reduce poverty but also to increase nutrient security, particularly on smallholder farms (De Luque & Creamer, 2014). The access to diverse, nutrient-dense food sources is consequently a priority in order to improve sustainable nutrient security, especially in low-income countries and to prevent hidden hunger (Nelson et al., 2018; Petry et al., 2015). Hidden hunger is generally concerned with a deficiency of nutrients and occurs when the food quality in a person's diet is insufficient for normal growth and development. Minerals, such as Fe and Zn, are thereby key determinants in staple crops and foods for sufficient dietary micronutrient uptake (Díaz-Gómez et al., 2017).

Common beans further present a much better source for these minerals in comparison to cereals (Castro-Guerrero et al., 2016). In common beans, the Fe concentration ranges from 35 to 90 μg/g with an average of 55 μg/g and is higher when compared to crops like rice (6.3–24.4 μg/g), wheat (25 μg/g–56 μg/g) or maize (9.6–63.2 μg/g). Breeding approaches have recently even achieved a Fe concentration of 130 μg/g (Kimani & Warsame, 2019). Common beans also have a relatively high Zn seed content (21–54 μg/g), with an average of 35 μg/g. Environmental and genotypes can, however, influence seed mineral concentrations as recently found with landraces and improved common bean varieties (Caproni et al., 2020; Hummel et al., 2018; Murube et al., 2021; Philipo et al., 2020). Although there is no statistically significant correlation between Fe and Zn content of seeds and the geographical distribution of bean (Caproni et al., 2020), previous studies provided evidence for a tendency for Andean pools to contain more Fe (Beebe et al., 2000) and Mesoamerican pools more Zn (Islam et al., 2002). Moreover, in a more recent study, new multi-parent populations were developed at the University of Nairobi. Lines harbouring different tolerance traits (drought, low soil fertility, major bean diseases) were combined with lines with high mineral traits (Fe and Zn). Eighty-four selected lines were more drought-tolerant and had more than 90% better yield compared to their parents. Forty-six promising lines had further higher grain Fe and also Zn concentrations compared with their parents. These lines can possibly now contribute to increased bean productivity and also combating micronutrient deficiencies in eastern Africa and other parts of Africa (Kimani & Warsame, 2019).

3 | HEALTH

3.1 | Impact on health

Pregnant women and children are specifically at risk in their health due to high mineral needs but poor mineral intake. While minerals are required by humans in small quantities, minerals participate in a wide variety of metabolic processes. Fe is, for example, required for the synthesis of haemoglobin and several hormones. A conventional breeding programme developed in Rwanda and in the Democratic Republic of Congo (DRC) already resulted in the selection of high Fe-containing common bean lines. These lines were also well adapted to the local conditions and suited both the farmers' and consumer preferences (Mulambu et al., 2017). The programme HarvestPlus of the Consultative Group for International Agricultural Research (CGIAR) particularly focuses on the selection of such Fe bio-fortified common bean lines (Asare-Marfo et al., 2013). African countries, followed by countries in Latin America, the Caribbean as well as Asia, rank, therefore, high on the list of countries targeted under the Biofortification Priority Index (HarvestPlus, 2020) (Figure 4). Such Fe-biofortified bean lines have already improved the Fe status and health of women in several African countries (Andersson et al., 2017; Haas et al., 2016). However, how these lines perform with regards to yield as well as nutrition under drought/heat stress conditions associated with climate change still remains to be investigated.

A previous study on diet modelling also found an association between bean consumption, improvement of nutrient intakes and healthy eating index scores (Hornick, 2007). Low-quality diets often lack dietary diversity along with high amounts of saturated fat and low vegetable, fruit, as well as fibre intake that can contribute to disease risk (Hiza et al., 2013). Consuming dry beans results in higher intake (10% or more) of fibre, protein, folate, Zn, Fe and Mg with lower intake of saturated fat and total fat which provides an improvement in the overall diet quality (Mitchell et al., 2009). Replacing refined carbohydrates in the diet with protein sources that are low in saturated fat, as in beans, reduces, for example, the risk of cardiovascular diseases (Hu, 2005; Mobley et al., 2014). People following a Mediterranean-style diet, richer in plant foods, including bean, have, indeed, a lower risk of cardiovascular disease and mortality (Estruch et al., 2006; Serra-Majem et al., 2006). The Dietary Guidelines for Americans (DGA, 2015–2020) (available at https://health.gov/our-work/food-nutrition/previous-dietary-guidelines/2015, accessed May 2021) further consider the beans' nutritional content

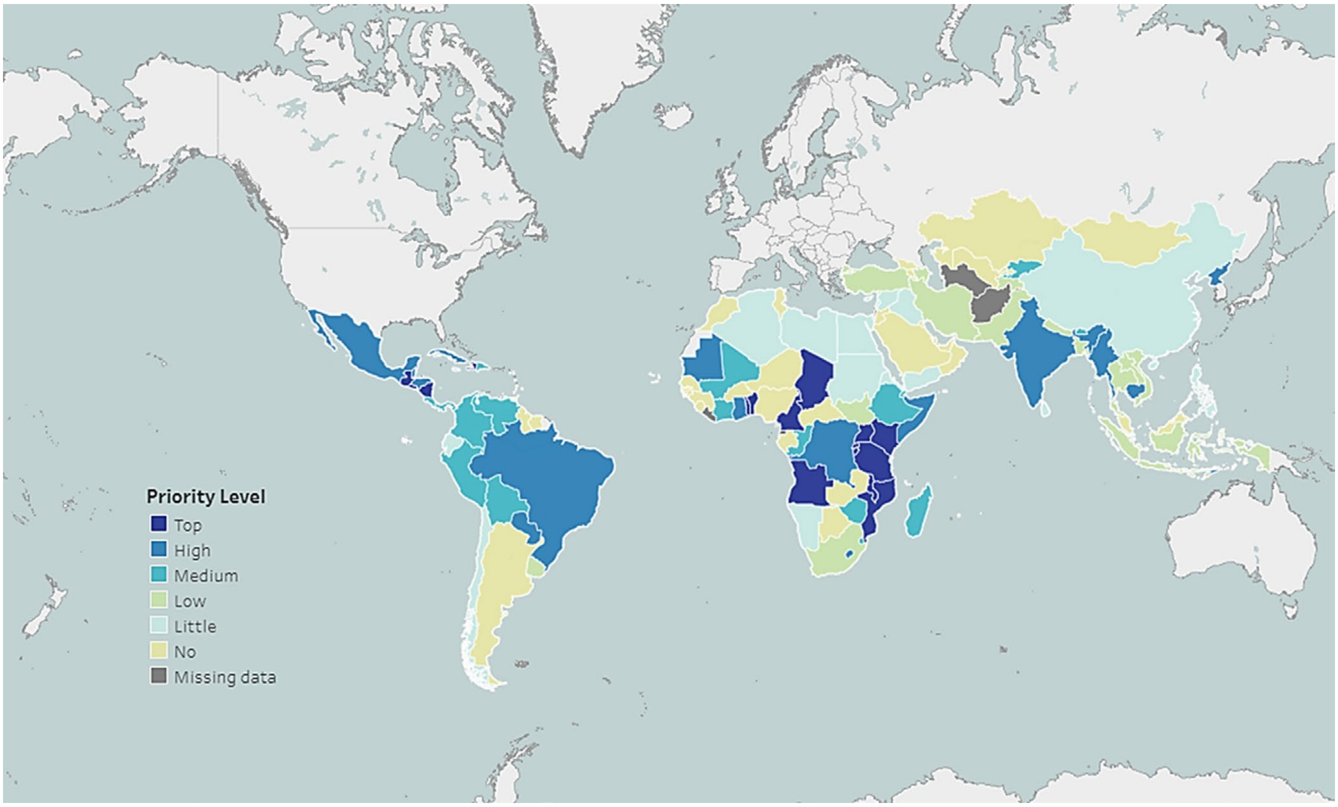

FIGURE 4 Common bean Bio-fortification Priority Index. Picture courtesy of HarvestPlus (https://bpi.harvestplus.org/bpi_cropmaps.html?id=c12021)

and benefit as both a protein and a vegetable. Beans can, therefore, be regarded as either in order to appropriately meet the recommended dietary intakes. The Guidelines on Nutrition and Physical Activity for Cancer Prevention advocates the consumption of poultry, fish and beans as an alternative to pork, lamb and beef while stressing the importance of vegetables (Kushi et al., 2012). The American Heart Association further recommends consuming 360 g of beans per week for adults for the prevention of cardiovascular diseases (Van Horn et al., 2016). However, the large consumption of bean seeds, as a "meat replacement" staple food in many countries of Africa, Central and South America and Southern Asia, has already contributed to nutritional problems.

Finally, it should not be overlooked that common bean seeds are also an important protein source (16–30%), despite being deficient in sulphur amino acids (methionine and cysteine). In particular for geographic areas, where a large part of the dietary protein is obtained from legumes, there is a need to increase the content of sulphur containing amino acids in legume proteins. Increasing the concentration of S-containing amino acids is, therefore, a current major research task (Saboori-Robat et al., 2019). Several legume proteins, including those of common bean seeds (e.g. 7S globulins, protease inhibitors, lectins), are now regarded not only as, but also functional ingredients (Carbonaro et al., 2015). Common bean seeds further contain no cholesterol and only low amounts of total and saturated fats. They are rich, however, in carbohydrates (up to 60%), especially starch and several vitamins (biotin, folic acid, niacin, thiamine and riboflavin). They are further an important source of dietary fibre (up to 37%) (Trinidad et al., 2010). Distinctive physiological roles have been attributed to the two different fibre fractions: soluble vs. insoluble. Soluble fibre, making up only a small part of the total dietary fibre, can assist in lowering cholesterol levels as well as decreasing the risk of heart diseases in regulating blood glucose levels. The regulation of intestinal function is affected by the insoluble fibre fraction. Studies have also produced evidence showing the protective effect of legume fibres against risk of developing colon cancer (Zhu et al., 2015, Wang et al., 2013; Campos-Vega et al., 2013). Due to this high fibre content, common beans can significantly contribute to the recommended dietary fibre intake of adult women (25 g/day) and adult men (38 g/day) (Dahl & Stewart, 2015).

3.2 | Antinutrients

Common beans are also a source, as other legumes, of bioactive compounds. Bioactive compounds in common bean seeds include oligosaccharides, lectins, phytates, enzyme inhibitors, phenolic compounds, complex polyphenols (tannins) as well as saponins. The presence of these compounds has promoted the nutraceutical use of legumes (Carbonaro, 2021). In spite of the well-documented antinutritional effects of some legumes, residual (i.e. below their toxic level) amounts of most biologically active compounds help in the prevention and management of severe diseases, such as cardiovascular diseases. These diseases mainly affect the world population of industrialized countries (Padhi & Ramdath, 2017). Hypercholesterolemia (Zhang et al., 2010), type-2 diabetes (Mattei et al., 2015) and cancer (Mitchell et al., 2009) are diseases which can be prevented. Selection to decrease the antinutritional substances have been already done for common bean varieties that are generally consumed. Cooking and processing are two methods that also inactivate trypsin inhibitors that are relevant antinutritional factors. These inhibitors reduce the digestion and absorption of dietary proteins (Avilés-Gaxiola et al., 2018). Removing antinutritional substances may, however, result in yield reductions as they also play an additional protective role in pathogen or insect resistance (Boulter, 1982). Varieties with a high content of heat-stable (non-protein) compounds, such as tannins and PA, pose further concern. This is because protein digestibility is lowered by high molecular weight tannins (Mr 500–5000), especially condensed tannins (proanthocyanidins). They form strong insoluble complexes with proteins. Moreover, the reactivity of some tannins, in particular those in common beans, increases after thermal treatment (Carbonaro et al., 1992). Tannins further adversely affect the absorption of trace elements, especially of Fe, but also of Zn and Cu, as a result of tannin–metal complex insolubilization, particularly after cooking (Carbonaro et al., 2001). As discussed below, it is now also well documented that the other major cation chelator in the seed is PA (reviewed by Petry et al., 2015). Finally, tannins, PA and saponins also interact with the absorption of fat-soluble compounds including fat-soluble vitamins and carotenoids.

4 | MINERALS/PA AND DROUGHT/HEAT STRESS

4.1 | Mineral/PA content

In order to provide sufficient minerals to millions of consumers, relying on common beans as part of their diet, a better understanding is needed of the effect that particularly drought/heat stress has on bean yield as well as on the bean's mineral and antinutrient content. In this regard, some knowledge already exists from characterizing lentils. Lentil plants exposed to drought and/or heat stress had lower amounts of vital minerals (K, P, Ca, Fe, Mn and Zn). This decrease was further associated with a reduction of root biomass under heat stress and a negative effect, due to drought stress, on transpiration, stomatal conductance as well as root function. When both stresses (drought and heat) acted simultaneously on lentil plants, the effect was even more profound (Sehgal et al., 2019). Choukri et al. (2020) also analysed 100 lentil genotypes from a global collection grown under normal, heat and combined heat–drought conditions. Fe, Zn and crude protein content was significantly reduced under these stress conditions. The effect of combined heat–drought stress was, however, more severe than by heat stress alone. A significant positive correlation also existed in lentils between Fe and Zn concentrations under both non-stress and stress conditions (Choukri et al., 2020).

Most efforts to improve the nutritional quality of common beans have up to now focused on developing varieties with lower amounts of antinutritional compounds, such as lectins (phyto-hemagglutinin L, phyto-hemagglutinin E), phaseolin and phytates, and a higher Fe and Zn content (Cominelli et al., 2020; Samtiya et al., 2020; Vasconçelos & Oliveira, 2004). For common beans, genotypic variation in the content of Mg, sulphur and Fe in bean leaves, and Ca and Fe in seeds have been reported in response to drought (Beebe et al., 2000). Smith et al. (2019) also found, by analysing a small number of 10 bred lines developed by CIAT, that drought can decrease the amount of minerals in the common bean soluble leaf fraction, but not within the seeds. A reduction in the concentration of Fe as well as phosphorus and Zn by 5–20% have been also reported for a still rather small number of bean lines/varieties under drought conditions (Hummel et al., 2018; Sehgal et al., 2018; Smith et al., 2019). A first multi-year field trial at a climate analogue site experiencing weather conditions, similar which has been predicted in year 2095 for Malawi, has also provided strong evidence that the amount of Fe significantly declines in common beans under drought conditions (Hummel et al., 2018). In contrast, when 20 bean varieties were tested, a significant increase in Zn, due to drought stress, has been measured (Hummel et al., 2018). While changing climatic conditions might, therefore, result in increased Zn-levels in future bean servings, these servings possibly have a lower Fe content and a higher amount of undesirable antinutrients, such as PA (Hummel et al., 2018; Nelson et al., 2018).

PA is the most abundant phosphorylated derivative of myo-inositol and the main storage form of phosphorus in the seed. PA also plays an important function in regulating different cellular processes and also limits oxidative stress (Sparvoli & Cominelli, 2015). The amount of PA, dependent on the phosphate concentration, mainly accumulates in the bean seed and in the cotyledons (95–98%), with only a small quantity found in the embryo and the seed coat (Blair, Herrera, et al., 2012). PA is further negatively charged and a strong mineral cation chelator. Any increase in the PA amount due to drought/heat conditions is, therefore, of great concern. In experiments carried out in the field with different common bean varieties under rain-fed and drought conditions, representing conditions forecasted by 2050 for south-eastern Africa by the EcoCrop climate impact modelling system, a significant increase in the PA amount in common beans exposed to drought stress was already found. This increase was from 0.96% under rain-fed conditions to 1.16% under drought conditions. Fe, Zn and PA under drought stress conditions at the field site were further influenced by weather conditions rather than genotype (variety) (Hummel et al., 2018). The underlying physiological basis for the PA increase under drought stress is, however, not well studied.

Since data are overall still contradicting and only based on a small number of lines and varieties tested, more in-depth investigations are urgently required to more exactly determine how drought and heat-associated reductions in yield also affects the nutrient quality of common bean seeds and the PA content. Such more detailed investigations should be carried out, however, not only under combined drought and heat stress conditions in a greenhouse but also under natural field conditions to more precisely determine the effect of intense natural drought/heat conditions on minerals and antinutrients.

4.2 | Mineral uptake and bioavailability

Fe accumulation is highest in leaves with increasing ferritin synthesis during plant development (Zielińska-Dawidziak, 2015). Ferritin functions as the main Fe-storing protein in the seeds of legumes, which has traditionally been the source of plant-derived ferritin (Marentes & Grusak, 1998). Relatively little is, however, currently known about Fe uptake and regulation in legumes, in particular under drought/heat stress conditions. This is despite several articles having recently reviewed Fe uptake and transportation in plants in general (Curie & Mari, 2017; Kobayashi & Nishizawa, 2012; Thomine & Vert, 2013). A large number of likely transport protein candidates have been already identified in legumes as more genome and transcriptome data of various legumes are becoming available. Members of the NRAMP, YSL, VIT and ZIP transport families have higher expression in legume root nodules. These members likely play a role in the transport of Fe across symbiotic membranes (Brear et al., 2013). The application of fertilizers, either to the soil or as a foliar spray, also significantly increases the accumulation of nutrients in the seed, but transport is hampered by limited mobility in the phloem sap (Bindraban et al., 2015).

Nutrients can be further relatively immobile, not only in plant tissues, but also in the soil. This immobility affects their transport within the phloem. A greater rooting depth is generally required for plants to access from the soil sufficient amounts of minerals (Maillard et al., 2015). Transporters, which are essential for the uptake of minerals from the rhizosphere, have been characterized in common beans (Castro-Guerrero et al., 2016). Fe and ferritin further accumulate in separate cellular locations in bean seeds. Fe primarily accumulates in the cytoplasm of cells surrounding the pro-vascular tissue, while ferritin, the major Fe-storing protein in legume seeds, accumulates in the amyloplast, as found for peas (Cvitanich et al., 2010; Marentes & Grusak, 1998). In common bean seeds, only 15% to 30% of total Fe is, however, ferritin bound. An excess of Fe and osmotic stress increases ferritin expression in common beans (Hoppler et al., 2014), but ferritin does, overall, not contribute much in the provision of Fe.

IRT-like transporters are further involved in the uptake of both minerals that are then mobilized to the shoots via the xylem and then delivered to developing tissues, including seeds, exclusively via the phloem (Hindt & Guerinot, 2012; Khan et al., 2014; Sinclair & Krämer, 2012). Fe uptake regulation is under the control of two transcriptional networks, FIT (At2g28160) and PYE (At3g47640), while Zn uptake requires bZIP transcription factors (Hindt & Guerinot, 2012; Sinclair & Krämer, 2012). The common bean genome contains putative homologs for the components of the networks (Phvul.005G130500/FIT1-like; Phvul.002G099700/IRT1-like; Phvul.003G086500/OPT3-like; Phvul.011G035700/bZIP23-like) (Castro-Guerrero et al., 2016). Furthermore, an Arabidopsis protein localized in the phloem, OPT3, is a component of the shoot-to-root signalling network. This protein, not yet characterized in more detail in common beans, passes on the Fe status in leaves to roots and *opt3* mutants accumulate more Fe and Zn in roots and leaves (Mendoza-Cózatl et al., 2014).

The presence of antinutritional compounds, such as PA and polyphenols, limits the bioavailability of minerals (Glahn et al., 2017; Petry et al., 2010; Tako et al., 2014). By adversely affecting the absorption of minerals, PA decreases the bioavailability of these minerals and, as a consequence, negatively impacts the nutritional value of seeds (Petry et al., 2015). The amount of PA has been further positively correlated with amounts of non-ferritin bound Fe (DeLaat et al., 2014). Polyphenols are also highly interconnected with mineral amounts (e.g. Fe). They are further involved in resistance to different types of stresses, in part due to their antioxidant properties (Herrera et al., 2019). A major obstacle to Fe biofortification in common beans is, therefore, low Fe absorption due to the presence of polyphenol(s) (Ganesan & Xu, 2017). Different subclasses of such polyphenols are present in common beans, mainly located in the seed coat. Although some polyphenols, such as kaempferol, kaempferol 3-glucoside, catechin and 3,4-dihydroxybenzoic acid, are able to promote Fe uptake, at least in an *in vitro* system, others have a strong inhibitory effect. This outweighs the effect of those compounds promoting an increase in Fe uptake (de Figueiredo et al., 2017; Hart et al., 2015). Unfortunately, to our knowledge, a serious gap is still the lack of any bean breeding programme specifically targeting polyphenols for reduction of any negative effects these polyphenols have particularly on Fe bioavailability and how drought/heat stress can affect this process.

5 | BREEDING USING “OMICS” TOOLS

Previous common bean research work, particularly on drought/heat tolerance, focused mainly on investigating and characterizing agro-morphological traits to identify bean lines with better plant growth under these stresses. Several different traits, for example pod harvest index, were thereby found to be associated with drought tolerance (Polania, Rao, et al., 2016). “Omics” tools (genomics, transcriptomics and proteomics) have been, or are currently, applied to identify and characterize genes and genome sequences in common bean plants that are involved in drought/heat stress tolerance or mineral production. These activities are aimed to produce improved common bean material for drought/stress tolerance and higher mineral content. A recent review has highlighted the achievements in common beans by applying “omics” tools (Nadeem et al., 2021).

Most of the recent/current advances made by applying “omics” tools were/are only achievable due to the publication of the common bean genome sequence (Schmutz et al., 2014; Vlasova et al., 2016). In contrast to the Andean common bean genome with an estimated size of 587 mega base pairs (Mbp) with ~27 thousand genes (91% clustered in synteny blocks with Glycine max), the Mesoamerican genome is 549.6 mega base pairs in size with ~30 thousand genes and 94% of which has been functionally annotated (Vlasova et al., 2016). The availability of the common bean sequence in 2014 has further offered the opportunity for better understanding drought adaptation and tolerance in common beans. However, previous studies never focused on a deeper level on any possible link between mineral accumulation and availability and drought/heat stress.

5.1 | Quantitative trait loci (QTL) identification

5.1.1 | QTLs for drought tolerance

Advances in genetic investigation using genomics paved in common beans the way not only to better understand genetic variation, for example within the European common bean germplasm and to trace its divergence from the American germplasm (Bellucci et al., 2021; Caproni et al., 2020; Lioi & Piergiovanni, 2013) but also for the identification and characterization of quantitative trait loci (QTL) related to agronomic and nutrient traits. QTL analysis generally links phenotypic and genotypic data. In particular, numerous QTL studies in common beans have been carried out to identify specific traits linking abiotic stresses—including drought—to agronomic traits of interest such as plant size, seed yield and flowering time. These approaches rely on the genetic analyses on crosses of susceptible x tolerant parental common bean genotypes, belonging to either a single gene pool, or both the Andean and Mesoamerican gene pools (Nadeem et al., 2021). The resulting population is then used to construct genetic linkage maps. The resolution of these maps has considerably improved over the years. Based on these maps, an increasing amount of genetic markers including microsatellites and single-nucleotide polymorphisms (SNPs), a variation at a single position in a DNA sequence, have been recently developed (Leitão et al., 2021; Sedlar, Kidrič, et al., 2020; Sedlar, Zupin, et al., 2020). Particularly, mining in common beans QTLs affecting field performance and nutrient value under drought will be still crucial in the future design of molecular tools for marker-associated selection (MAS). Mining will also be crucial for the identification of possible molecular targets important for gene editing (GE) approaches, as recently described for wheat grown in dry and hot environments (Tura et al., 2020). QTLs related to yield, flowering time as well as days to maturity, were specifically identified in common beans based on the genetic analysis of a Mesoamerican x Mesoamerican drought-tolerant x susceptible cross (Blair, Galeano, et al., 2012). In addition, QTLs related to seed yield and flowering time have been recently identified after crossing two Andean genotypes reacting differently to drought stress (Dramadri et al., 2019). Three loci related to seed yield per plant (Syp1.1, Syp1.2, Syp2.1) are of specific interest for yield-oriented MAS under drought stress with Syp1.1 emerging as a master regulator of yield under drought (Sedlar, Zupin, et al., 2020; Trapp et al., 2015). Moreover, a great number (189) of QTLs have been found related to seed weight and 33 QTLs related to yield. Many of these QTLs are within—or in proximity—to genes known to be involved in primary or specialized metabolism (Valdisser et al., 2020). Finally, a stable QTL related to yield (Yd4.1) has been recently identified in a common bean BAT881 × G21212 RIL population tested in field trials across four different locations in Colombia. This QTL is not only associated with drought stress, but also to phosphorus and Al stress. The molecular function of Yd4.1 is, however, still unknown (Diaz et al., 2018).

Further, SNPs determination in common beans allowed to annotate a SNP to a gene related to drought tolerance. This SNP is related to biosynthesis of proline, a well-known osmotic protector (Villordo-Pineda et al., 2015). A most recent SNP analysis under drought conditions also identified SNPs for processes responsive to drought stress. These processes included stomatal regulation, protein translocation across membranes, redox mechanisms, hormone as well as osmotic stress signalling (Leitão et al., 2021). A further more recent whole-genome resequencing-derived SNP dataset applied for a genome-wide association analysis identified 12 loci. These loci were significantly associated with survival after drought stress at the seedling stage. They also confirmed the drought-related function of an aquaporin gene (PvXIP1;2) located at Locus_10 (Wu et al., 2021). Finally, a good example of what can be achieved by applying the QTL technology in legumes has been recently shown for chickpea and cowpea. Genetic physical maps were developed and QTLs including “QTL-hotspot” regions containing QTLs for several drought tolerance traits were identified. This analysis has already resulted in 29 new cowpea varieties developed and the production of 20,353 t of certified seeds which have been planted on about 508,825 ha (Varshney et al., 2019).

5.1.2 | QTLs for mineral (Fe) content

Studies about the genetic basis of common bean seed composition have so far mainly focused on minerals, such as phosphorus, Fe and Zn, due to their problems related to deficiency in human diets. Identification of QTLs was thereby based on the application of both inter and intragene pool populations (Casañas et al., 2013). A recent genome-wide association studies (GWAS) resulted in the identification of quantitative trait nucleotides (QTNs) associated with seed content of nitrogen, phosphorus, Ca, Mn and Zn, while no significant associations were found for Fe content (Gunjača et al., 2021). In contrast, Blair, Galeano, et al. (2012) found numerous QTLs, also related to Fe, although usually found to be population or environment specific. QTLs associated to seed phosphate content have been identified in a RIL common bean population (intragene pool Andean x Andean) on chromosomes Pv02, Pv05, Pv06, Pv05 and Pv11, with additional PA-related

QTLs on Pv04 and Pv08 (Cichy et al., 2009). P-QTLs derived from the analysis of intergene pool populations (Mesoamerican x Andean). Loci associated to seed phosphate and total phytates were identified on Pv02, Pv03, Pv04, Pv06, Pv10 and Pv11 (Blair, Galeano, et al., 2012). An intergene pool study based on a Mesoamerican × Andean cross further identified QTLs associated with both Fe and Zn content. QTLs were scattered along chromosomes Pv03, Pv04, Pv06, Pv07, Pv08, Pv09, with a cluster of 5 on Pv11 (Blair et al., 2010). Furthermore, overlapping Fe and Zn-QTLs were identified on a linkage group located on Pv06, alongside QTLs located on Pv03, Pv04, Pv07, Pv08 and Pv11 (Blair et al., 2010). A recent meta-analysis, conducted on the cited literature, finally reduced the original set of detected QTLs into a set of 12 QTLs, with two QTLs specific for Fe and Zn, and 8 QTLs related to both (Izquierdo et al., 2018).

Interestingly, a recent study has presented the first common bean MAGIC population of the Mesoamerican gene pool (Diaz et al., 2020). The study allowed the identification of different genomic regions associated with yield, mineral accumulation, phenology and physiological traits under drought conditions. Moreover, major QTLs controlling more than one trait, even in different seasons, and candidate genes for major QTLs were identified. This study now provides interesting data for the development of advanced breeding tools. In a further recent development, optimal contributions selection was applied to design common bean crossings within four market groups with relevance for East Africa. Genomic estimated breeding values were thereby predicted for grain yield, cooking time, Fe, and Zn in an African bean panel of 358 genotypes in a two-stage analysis. Such genomic selection using optimal contributions selection will possibly accelerate breeding of high-yielding, biofortified, and rapid cooking African common bean cultivars (Saradadevi et al., 2021).

5.2 | Biotechnology

"Biotechnology" to improve common beans was already suggested in 2003 (Svetleva et al., 2003). Plant biotechnology generally allows precise genetic changes by integrating, for example, an identified and characterized gene providing a beneficial trait into the plant genome or to change a gene inside a plant by genome editing (Du et al., 2016). The process to obtain either a transgenic genetically modified plant (GMO) or gene-edited plants generally involves as tools application of plant transformation to insert a gene sequence, in vitro culture of transformed plant tissues as well as whole plant regeneration. Although potential genes for transformation are known, due to an available sequenced common bean genome with 94% of genes functionally annotated (Vlasova et al., 2016) allowing to identify target genes for any desirable trait modification, efficient bean transformation to obtain transformed modified plants has still technical limits. Common bean transformation is by far not a routine approach, as in other species (De Paolis et al., 2019). However, first examples of possible successful genetic modification of common beans include overexpression of a methionine-rich storage albumin from Brazil nut in transformed bean plants after particle bombardment of the apical meristematic region of embryos for gene transfer (Aragão et al., 1999). Expression of the barley (*Hordeum vulgare*) late embryogenesis abundant protein (HVA1) in transformed common beans is a further example where the method of particle bombardment of the shoot meristem for transformation was applied (Kwapata et al., 2012). Produced transformed plants were more drought-tolerant due to longer roots. These examples provide overall evidence that plant transformation is, indeed, applicable for bean biofortification.

5.2.1 | Genes and drought/heat stress tolerance

Blair et al. (2011) already characterized 4219 unigenes from cDNA libraries prepared from contrasting drought-treated common bean genotypes. By applying suppression subtractive hybridization (SSH) and a whole-genome protein database for target hits, transcription factors (NAC and AP2-EREBP family) and genes involved cell metabolic processes and present in photosynthesis were further identified to be involved in the drought response of common bean (Müller et al., 2014; Recchia et al., 2013; Wu et al., 2016). Table 2 shows a selection of genes which have been so far investigated regarding drought stress in common beans. When further drought responsive genes in leaf and root tissue of common bean were investigated by RNA-Seq, genes were predominantly involved in oxidative stress. This suggests a tolerance mechanism based on reduction of damage from reactive oxygen species (Pereira et al., 2020). Orthologues of the soybean Hsp20 genes are further up-regulated in response to drought and salinity stress (Lopes-Caitar et al., 2013). López-Hernández and Cortés (2019) recently identified in common beans by coupling genome–environment associations with last-generation genome wide association study algorithms candidate genes including HSP20, but also MED23, MED25, HSFB1 and HSP40 that are directly linked to heat-responsive pathways. Additional candidate genes

TABLE 2 Stress responsive genes and their function in common beans

Study	Function	Description	Dry bean accession	Homologue accession/ species
Transcriptome analysis of differentially expressed genes in roots of BAT 447 under drought stress during development (Recchia et al 2013)	NAC transcription factor (TF)	NAC domain protein, IPR003441	|75749297|	|224088037| *Populus trichocarpa*
		NAC4 protein	|75748424|	|62546189| *Glycine max*
		NAC domain protein	|75749318|	|224088037| *P. trichocarpa*
		NAC domain protein	|75748418|	|187940303| *G. max*
	DREB TF	Fe-S cluster assembly protein DRE2 homolog	|75749717|	|292630743| *G. max*
		DREB	|75748469|	|32480821| *G. max*
	ERF TF	Ethylene-responsive element binding factor 4	|75749028|	|190361165| *G. max*
		Transcription factor EIL2	|75749407|	|18643339| *Vigna radiate*
	bHLH TF	Coiled-coil-helix-coiled-coil-helix domain containing protein	|75749257|	|66947630| *Medicago truncatula*
	bZIP TF	Transcription factor bZIP70	|75749123|	|145652341| *G. max*
		Leucine-rich repeat protein	|75748580|	|223452524| *G. max*
		TGA-type basic leucine zipper protein	|75748298|	|15148922| *Phaseolus vulgaris*
		F-box/LRR-repeat protein, putative	|75748883|	|255558466| *Ricinus communis*
	MYB	MYB transcription factor MYB185	|75748729|	|110931684| *G. max*
	GATA-factors	GATA transcription factor, putative	|75748743|	|255572876| *R. communis*
	WRKY family	WRKY36	|75748775|	|151934195| *G. max*
	Ubiquitous factors TFIIA e Sp1	Transcription initiation factor ia, putative	|75748702|	|255566898| *R. communis*
	IAA (auxin-responsive)	Auxin-responsive protein IAA1, putative	|75748737|	|255552973| *R. communis*
		Auxin-responsive family protein	|75748789|	|15226425| *Arabidopsis thaliana*
	GRAS	GRAS family transcription factor	|75748648|	|224106445| *P. trichocarpa*
		GRAS family transcription factor	|75749650|	|224106445| *P. trichocarpa*
	Heteromeric factors	Transcription factor CCAAT	|75748712|	|193237557| *Lotus japonicas*
	eIF2—alpha family	Translation initiation factor EIF-2b	|75748325|	|255544025| *R. communis*
		Eukaryotic translation initiation factor 5A	|75748617|	|20138704| *Manihot esculenta*
	Zinc finger	C2-H2 zinc finger protein	|75749674|	|161087182| *G. max*

(Continues)

TABLE 2 (Continued)

Study	Function	Description	Dry bean accession	Homologue accession/ species
Transcriptome analysis of differentially expressed genes in BAT 447 under drought stress during flowering (Müller et al. 2014)		Uncharacterized protein LOC100305788		|351721030| *G. max*
		Oxygen-evolving enhancer protein		|*358344003*| *M. truncatula*
		Chlorophyll *a*/*b* binding protein type II		|*16805332*| *G. max*
		Hypersensitive induced reaction protein 1		|354683205| *G. max*
		Invertase/pectin methylesterase inhibitor family protein		|*297310623*| *Arabidopsis lyrata*
		Auxin-repressed protein		|*357446689*| *M. truncatula*
		Predicted: 40S ribosomal protein S17-4		|*356521554*| *G. max*
Transcriptome analysis of differentially expressed genes in BAT 447 under drought stress during grain filling (Müller et al. 2014)		Predicted: 40S ribosomal protein S16-like		|*356524632*| *G. max*
		Leucine zipper protein		|*357491217*| *M. truncatula*
		Unknown		|*388517649*| *L. japonicus*
		Predicted: cell wall/vacuolar inhibitor of fructosidase 1-like		|*502150782*|*Cicer arietinum*
		NAD-dependent isocitrate dehydrogenase		|*3790188*| *Nicotiana tabacum*
		Predicted: RING-H2 finger protein ATL66-like		|356539989| *G. max*
Transcriptional analysis of drought induced genes in the roots of BAT 477 (Recchia et al. 2013)	Cellular metabolism	Pyruvate decarboxylase, putative		|255579310| *R. communis*
		Malate dehydrogenase-like protein		|83283965| *Solanum tuberosum*
		Glyceraldehyde-3-phosphate dehydrogenase		|255638912| *G. max*
		Glutaredoxin-1, grx1, putative		|255540625| *R. communis*
	Biological processes	Spliceosomal complex		|224094081| *P. trichocarpa*
		Methionine adenosyltransferase		|75304713| *Phaseolus lunatus*
		S-adenosylmethionine decarboxylase		|156181612| *P. vulgaris*
		Methionine adenosyltransferase		|75304713| *P. lunatus*
	Abiotic stress response	Interferon-related developmental regulator family protein		|42571665| A. thaliana
		Light-inducible protein ATLS1,		|192910730| *Elaeis guineensis*

TABLE 2 (Continued)

Study	Function	Description	Dry bean accession	Homologue accession/ species
		Group 3 late embryogenesis abundant protein		|75708857| *P. vulgaris*
		Proline-rich protein		|806310| *G. max*
		LEA5		|1732556| *G. max*
		LEA protein		|1350522| *Picea glauca*
		LEA5		|1732556| *G. max*
	Biotic stress response	Isoflavone synthase 1		|184202203| *Vigna unguiculate*
		Isoflavone synthase 1		|184202203| *V. unguiculata*
		PvPR2		|130835| *P. vulgaris*
	Transport	Plastidic phosphate translocator-like protein1		|61651606| *Mesembryanthemum crystallinum*
		Cation:cation antiporter		|255587991| *R. communis*
		ATP binding protein,		|255552798| *R. communis*
		Calcium ion binding		|255637247| *G. max*
Transcriptional response to drought stress in roots and leaves of drought-susceptible and drought tolerant common bean genotypes (Pereira et al. 2020)		Aquaporin NIP	Phvul.006G171000	
		Peripheral-type benzodiazepine receptor and related proteins	Phvul.001G205900	
		DNAj homolog subfamily c member	Phvul.006G060700	
		Beta-fructofuranosidase	Phvul.005G158500	
		Class IV chitinase, insoluble isoenzyme WINV1-related	Phvul.005G155800	
		Protein phosphatase 2C	Phvul.001G075400	
		Glutathione S-transferase	Phvul.008G113700	
		Heat shock transcription factor	Phvul.007G061800	
		Late embryogenesis abundant (LEA) group 1	Phvul.007G259400	
		Linoleate 13S-lipoxygenase.	Phvul.002G228700	
		MYB-like DNA-binding domain	Phvul.002G184600	
		No apical meristem (NAM) protein	Phvul.005G084500	
		NADH oxidoreductase-related	Phvul.003G131500	
		Peroxidase	Phvul.009G140700	
		Glycosyl hydrolase family 10	Phvul.009G120500	

involved in the response of common bean to water deficit (drought) conditions were very recently identified from a collection of more than 150 Portuguese common bean accessions (Leitão et al., 2021).

5.2.2 | Genes and mineral (Fe) content

"Omics" tools have also been applied in order to increase the mineral content and bioavailability of common beans. The first important step in lowering the production of PA in common beans has been the isolation and sequencing of genes involved in PA biosynthesis and transport (Fileppi et al., 2010; Panzeri et al., 2011). Recently, additional putative biosynthesis and transport genes have been further identified (Cominelli et al., 2017; Cominelli, Pilu, et al., 2020). The availability of this data will now allow new cutting-edge innovative research, including epi-genomics and translatome analysis. Two identified allelic common bean mutants, affecting the PvMRP1 PA transporter, caused a 75–90% reduction in the PA content (Campion et al., 2009; Cominelli et al., 2018; Panzeri et al., 2011). Particularly, the mutant bean line, *lpa1*, has a 25% reduction in raffinosaccharides, the sugars causing flatulence. The biosynthesis of these sugars is strictly linked to the biosynthesis of PA. A study with human volunteers further found that seeds from the *lpa1* mutant line provides better Fe absorption, compared to a non-mutant line (Petry et al., 2014). When applied in common household recipes, *lpa1* mutant seeds had, however, a lower retention of Zn. Due to a hard-to-cook phenotype, associated with the increased thermal stability of lectins in the *lpa1* mutant lines, adverse gastrointestinal symptoms occurred (Petry et al., 2016). The effect of the *lpa1* mutation on thermal stability of seed lectins is, however, only problematic in a genetic background which contains phyto-hemagglutinin L. In contrast, no significant effect on thermal stability has been found when the genetic background contains both phyto-hemagglutinin-L and phyto-hemagglutinin E, which most common bean genotypes have (Cominelli, Galimberti, et al., 2020; Cominelli, Pilu, et al., 2020).

When developing *lpa* mutants, the essential role of PA as regulator of cellular processes in plant vegetative tissues has to be considered in order to avoid important undesirable pleiotropic effects (Sparvoli & Cominelli, 2015). Importantly, the common bean *lpa1* mutant has no reduced germination or any reduced plant growth and fertility. Still lacking is, however, a much more detailed morphological/physiological evaluation of such common bean *lpa1* mutants. Cereal *lpa* mutants, the first *lpa* mutants isolated, have received so far very little interest. They are affected in the transporter orthologues of PvMRP1 (Colombo et al., 2020; Sparvoli & Cominelli, 2015). These cereal mutants have further a reduced yield (5–10% decrease) and non-optimal field performance (Raboy, 2020). In contrast, the *lpa1* common bean mutant has no such negative agronomic effects under field conditions (Campion et al., 2009; Chiozzotto et al., 2018). However, field studies are urgently required to assess the potential of this mutant particularly under field conditions in much more depth. They would be also interesting for breeding programmes aimed to develop beans with increased mineral bioavailability and mineral content as well as lower concentrations of certain polyphenolic compounds (Hummel et al., 2020). Molecular markers for the *lpa1* and also *lpa12* bean mutants have been already developed. Such markers can now be applied in marker-assisted selection of common bean breeding lines as well as the evaluation of the performance of such lines with either individual or combined traits (Cominelli et al., 2018; Panzeri et al., 2011). However, some concern with the use of *lpa* beans still exists. PA, as a broad-spectrum antineoplastic agent, can act in cancer development and progression (Vucenik, 2019), despite the fact that no phytate has been detected in human biofluids (Wilson et al., 2015). Consequently, *lpa* beans may be particularly useful in areas where micronutrient deficiencies are prevalent. In contrast, crops with high amounts of phytates can also be beneficial for health in societies that have in their diet sufficient Fe available, but where both obesity and cancer are on the rise (Blair, 2013).

The exact role and function of PA in drought/heat tolerance is, however, still unclear. So far only known is that some low phytic acid (*lpa*) mutants are more drought sensitive (Cerino Badone et al., 2012). An Arabidopsis thaliana *mrp5* mutant (an *lpa* mutant; Nagy et al., 2009) and common bean *lpa1* mutants, affected in the AtMRP5 and PvMRP1 orthologous genes, have so far found to have some better drought tolerance (Chiozzotto et al., 2018; Colombo et al., 2020; Klein et al., 2003). Arabidopsis *mrp5-1* mutant rosette leaves have, in this regard, closer stomata to prevent water loss, and have a reduced transpiration rate and improved water use efficiency (Klein et al., 2003).. More drought tolerance of the common bean *lpa1* mutant is also evident under symbiosis. Transcriptional data provide evidence of higher expression of stress-related genes in the nodules and bacteroids of *lpa1* mutants when compared to nodules from non-mutant plants (Chiozzotto et al., 2018).

Finally, results with the *lpa1* mutant plants now open a new perspective in obtaining mineral improved common bean varieties. These varieties should not only better cope with drought/heat stress but also provide beans with a low PA content (Raboy, 2020). Introgression of these mutations into cultivated bean varieties is, consequently, a current major research task (Campion et al., 2009; Cominelli et al., 2018; Mulambu et al., 2017). This task also includes the evaluation of the performance of such lines, with either individual or combined traits, under environmental stress conditions. Common beans cooking and nutritional properties will also be evaluated in more depth in a quest to develop bio-fortified common bean lines devoid of negative traits (Cominelli, Galimberti, et al., 2020).

5.2.3 | Gene editing

Genome editing (GE) applying the clustered regulatory interspaced short palindromic repeats editing (CRISPR)/Cas system have already been applied to edit certain target genes in legumes (Bhowmik et al., 2021; Ji et al., 2019; Liu et al., 2019). GE is currently an effective "omics"-based tool in the manipulation of traits in crops (Du et al., 2016; Tiwari et al., 2020). While CRISPR is usually considered as a tool to generate double strand breaks, and consequently generate knock-out mutations, the modular nature of the CRISPR technology allows alteration of transcriptional activity, or epigenetic status, at a chosen target site (Lee et al., 2019). This can be achieved with a nuclease-deficient version system (dCas9), which can be tied to a diverse array of epigenetic effector domains for site-specific epigenetic modifications (Pulecio et al., 2017). The current advancements and limitations of GE, particularly in orphan crops, have been recently discussed by Venezia and Creasey Krainer (2021). Innovative techniques, such as GE and speed breeding, might effectively also shorten the time to develop drought-resilient common beans and consequently limit any risk of global food insecurity (Bhowmik et al., 2021). In particular, the development of alternative *lpa* common bean mutant lines by applying GE could prove valuable in the pursuit of improving specifically the nutritional value of common beans. Mutations in the rice OsSULTR3;3 gene, encoding type-3 sulphate transporters, have already resulted in rice *lpa* mutants that, in addition to reduced levels of PA, had changes in the amount of a broad spectrum of compounds such as amino acids, organic acids (e.g. citric acid) and other nutritionally relevant compounds including γ-aminobutyric acid (Zhou et al., 2018).

6 | AREAS FOR FUTURE EXPLORATION

To achieve the overall goal of higher common bean yield and dietary quality under changing climatic conditions will certainly require the establishment and application of an integrated research framework. This framework should consist of genomics, systems biology, physiology, as well as modelling and breeding (Palit et al., 2020). Recent advances in sequencing and phenotyping methodologies, the rapidly emerging genetic and genomic resources as well as integrated crop modelling and predictions of climate impacts, supports the establishment of a framework also for common beans. Exploring in more depth how landraces cope with drought/heat stress and why they seemingly have a higher mineral content (especially Fe and Zn) and protein than modern varieties (Celmeli et al., 2018) and how to produce more efficiently GMOs should also be part of the research activities. In addition, production of more annotated genomes will be very helpful to support any future transcriptomic, proteomic as well as epi-genomic data-mining efforts (Li et al., 2017). Finally, exploring the interesting idea of common bean rewilding, which is the reintroduction of specific traits from wild lines into the genetic background of commercial cultivars, should be part of the activities. Although whole-genome sequence data exist for numerous legume species, including common bean, next-generation sequencing (NGS)-driven improvements have not kept pace with that of cereal crops (Rehman et al., 2019). NGS would, for example, support the rewilding idea. Rewilding will specifically address the loss of diversity during the bean's domestication process and will possibly allow improving the bean's nutritional value and tolerance to stresses (Cowling et al., 2015).

6.1 | Exploring drought/heat stress tolerance

For most grain legumes, breeders mainly investigated in the past consequences of drought/heat stress on above-ground traits. However, investigating the relationship between below and above-ground traits by studying in the future in more depth will be an important aspect (Sofi et al., 2021). The application, specifically of proteomics as an "omics tool", will particularly allow to explore proteins involved in drought/heat tolerance and mineral production. Such proteomics studies will allow us to also investigate how these proteins are regulated (Zargar et al., 2017). Furthermore, specific target genes require more in depth investigation. Genes include the orthologous forms of the *Arabidopsis thaliana* and *Vitis vinifera* MYB60 genes. These genes, not well characterized in common beans, have been already extensively characterized for their specific role in the modulation of stomatal movement (Cominelli et al., 2005; Galbiati et al., 2011). Other possible target genes to explore are regulatory genes controlling the expression of DREB genes and that are activated by drought stress (Marcolino-Gomes et al., 2014).

6.2 | Improving mineral availability

An important future research priority is increasing mineral (Fe)-bioavailability in common beans. Fe biofortification in common beans requires, however, adequate Fe partitioning between plant tissues. The Fe, and also Zn, uptake mechanism as well as mobilization to allocate more Fe and Zn into bean seeds is, therefore, an area to be explored in more depth, particularly under drought/heat stress conditions. Specifically, IRT-like transporters involved in the mineral uptake can be thereby investigated. Since these transporters are also under the control of two transcriptional networks, these networks can be specifically characterized for how drought/heat stress affects these networks. Furthermore, isolation and characterization of the protein OPT3, a component of the shoot-to-root signalling network passing on the Fe status in leaves to roots, is a worthwhile target for more in depth investigation.

Different possible bio-fortification strategies to increase amounts of minerals have been already reviewed by White and Broadley (2009). Fe biofortication might also include the future isolation of common bean genotypes low in PA content. To our knowledge, no extensive variability for the PA trait, as found in mung beans (Dhole & Reddy, 2015), has been so far described for common beans. Only two *lpa* mutants have been isolated and characterized in common beans (Campion et al., 2009; Chiozzotto et al., 2018; Cominelli et al., 2018; Panzeri et al., 2011). Selection of more low PA bean mutant lines would, therefore, be a promising strategy to increase bioavailability of Fe, and also Zn (Petry et al., 2016; Raboy, 2020).

Efficient Fe accumulation in a bioavailable form is an interesting area to explore. Biofortification of edible plants by overexpression of a native ferritin gene applying the GMO technology is an interesting strategy to increase the Fe content in bean seeds. But, as shown in banana, a high ferritin concentration has to be achieved sufficient for food fortification (Yadav et al., 2017). In vacuoles, small Fe and Zn binding molecules, such as nicotianamine and organic acids (malate and citrate), have been further found as possible further targets for mineral biofortification (Hoppler et al., 2014). Mineral (Fe) bioavailability can, however, also be enhanced through improved processing procedures including soaking, thermal treatments, fermentation and/or germination. Combining popular traditions with innovative treatments, such as germination, is, therefore, an interesting alternative strategy to pursue. Germination and fermentation are thereby useful for increasing the activity of polyphenol-degrading enzymes and endogenous phytases, which limit the PA content (Carbonaro et al., 2001). Heating promotes, for example, denaturation and hydrolysis of proteins, influencing chelating capacity and significantly modifies the bio-accessibility of minerals (de Oliveira et al., 2018). More research is, however, needed to establish the effect of such processing procedures on mineral (Fe) bioavailability.

Modification in protein solubility and digestibility is a further process which can be explored. Such modification will affect mineral bioavailability (Carbonaro et al., 2005; Iddir et al., 2019). Diet modelling would, likewise, be an excellent approach to also capture the complexity of a diet as a whole (Mertens et al., 2017). Another important component is evaluating the effect of traditional cooking practices on the chemical- and nutritional composition of any selected bean lines. Further, evaluating how ingredients of traditional recipes can contribute to the composition of a balanced and a high nutritional-quality dish with a particular emphasis on minerals would be interesting to explore (Durazzo et al., 2019; López et al., 2013).

6.3 | Controlling antinutrients

A future challenge is to explore how to obtain more Fe without affecting the amount of antinutrients and of non-essential toxic elements, e.g. cadmium and nickel. These toxic elements, naturally present in trace amounts in the soil, enter the roots via the Fe-regulated transporter-1 mediated Fe/Zn uptake mechanism (Khan, Bouraine, et al., 2014). If any possible increases in the Fe content will also affect the PA content, particularly under abiotic stress conditions, has to be answered. Very few studies have so far investigated this aspect (Campos-Vega et al., 2010; Carbas et al., 2020). In addition, breeding material with specific polyphenol and tannin profiles should be developed with the aim to reduce their negative effect on Fe bioavailability and to more clearly define their function in Fe bioavailability. Also explored should be if antinutritional proteins, such as protease inhibitors, which are expressed as a response to environmental stress, will influence the Fe content of common bean seeds (Farooq et al., 2018). Giuberti et al. (2019) already found that absence of phaseolin, the main reserve globulin in seeds, with presence of the α-amylase inhibitor is a potential determinant for raising Fe, and also Zn, concentrations in common bean seeds. Introgression of the *lpa* mutation into the above genetic background is thereby an interesting idea to even allow greater improvement of Fe availability.

In summary, any mineral (Fe) optimized beans, which are developed in future bio-fortification programmes, should ultimately also resilient to stresses associated with climatic changes currently threatening future common bean production. Such newly developed common bean varieties should ideally maintain high yields but also have high amounts of minerals while having low amounts of antinutrients, such as PA, under drought/heat stress conditions. So far, the impact of drought/heat stress on common bean yield in combination with the effect of stress also on the mineral content of beans has, unfortunately, not been extensively investigated, particularly not under any field conditions. Lack of such field investigations is a major hurdle in the development of common bean varieties improved in drought/heat stress tolerance as well mineral content. Such field investigations are, therefore, urgently required.

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