

Asif M. Iqbal Qureshi
Zahoor Ahmad Dar
Shabir Hussain Wani *Editors*

Quality Breeding in Field Crops

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Foreword



Improving crop plants for enhanced quality of produce through conventional and modern plant breeding approaches is apt at this moment. Most of the conventional breeding experiments indicated that yield and quality traits are negatively correlated. However, with the advent of genomic resources and next-generation sequencing technologies, research can be directed towards precise understanding of the target genes responsible for controlling important quality traits. Systematic research and deployment of modern technologies including molecular breeding, genetic engineering, and genome editing will lead to development of high-yielding crop varieties with quality improvement. This informative book provides state-of-the-art information on improving nutritional quality in field crops such as maize, rice, wheat, pearl millet, soybeans, legumes, potatoes, and oilseed crops. With contributions from leading authorities in the field, this book will bring you up to date on the uses of conventional plant breeding and modern biotechnologies for improving the quality of important food, feed, and fibre products.

This book is a timely reference material and will be of great importance for a large number of scientists, students, and policymakers, who will find a common reference to discuss ways that plant breeding can be beneficial to all. I appreciate the untiring efforts made by Dr Asif Mohammad Iqbal Qureshi and his co-editors for bringing out this outstanding book on *Quality Breeding in Field Crops* for the reputed Springer Publishers. The authors deserve commendation and congratulations for their efforts. I am sure that the contents covered in this book will serve to satisfy the needs of scientists and scholars engaged in upgrading the quality of agricultural produce.

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Preface

The long-term objective of plant breeding remains at increasing productivity to meet the food requirements of people; however, with today's world of nutraceuticals, an essential component of economic yield lies in its quality. The breeding for improved nutritional quality has played a pivotal role in solving the problem of malnutrition especially for the community, including animals. However, with the advent of modern plant biotechnological tools, high precision has been achieved with higher-quality standards particularly since last decade; numerous accomplishments have been made in developing crop varieties with improved nutritional quality, which are summarized in this book. Thirteen chapters are written by globally reputed researchers and academicians in the field of crop improvement research (specific crop).

Chapter 1 is an overview of general nutritional aspects and genomic interventions for biofortification of field crops. The concept of markers and various commonly used molecular markers in cooking and eating quality of rice is discussed in detail in Chap. 2, while genetic modification for improving nutritional value of potatoes is presented in Chap. 3. Chapter 4 addresses conventional and molecular perspectives, highlighting bio-fortification of pearl millet, while Chap. 5 is focussed on common bean nutritional quality using genetic approaches. The beta-carotene-rich maize hybrids pursued by breeders using MAS are detailed in Chap. 6. The historical perspectives, highlighting the contributions by researchers for improving the fatty acid profile of soybean oil, are presented in Chap. 7. Chapter 8 is devoted to issues pertaining to breeding for cooking and canning quality traits in dry beans. Chapter 9 provides insight on genomic approaches in wheat for improved iron and zinc content, and the discussion includes the dependence of plant breeding on heritable variation. Improved grain and nutritional qualities are discussed in Chap. 10, whereas Chap. 11 is devoted to discussing the development of high tryptophan maize, and end-use quality in wheat is presented in Chap. 12. Lastly, quality value of oilseed Brassicas using molecular tools is discussed and detailed in Chap. 13.

Through this multi-authored book, an effort has been made to assimilate the most topical results about quality improvement in crop plants, which will be prodigious as reference material for researchers, teachers, and graduate students involved in quality

breeding in crop plants using conventional and modern biotechnological tools by unfolding principles of lately developed technologies and their application in improvement of crop plants. We express sincere thanks and gratefulness to our revered authors; without their untiring efforts this book would not have been possible. We are also thankful to Springer Nature for providing such opportunity to complete this book project.

Srinagar, Jammu and Kashmir, India

Asif M. Iqbal Qureshi
Zahoor Ahmad Dar
Shabir Hussain Wani

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About the Editors



Asif M. Iqbal Qureshi received his Ph.D. in Genetics and Plant Breeding from SKUAST Kashmir, India, in 2010. After his Ph.D., he worked as a senior research fellow in the NAIP sponsored project on saffron for two and half years. He was selected as an Assistant Professor in Genetics, Plant Breeding, and Biotechnology in Bihar Agricultural University, Sabour, Bihar, in 2012. Subsequently, Dr. Qureshi was selected as an Assistant Professor (GPB) and took over as principal investigator of the All India Coordinated Research Project Rapeseed-Mustard at SKUAST Kashmir in 2013. His work was recognised in the form of best centre award under the All India Coordinated Research Project Award (2015) by the Directorate of Rapeseed-Mustard, Bharatpur, Rajasthan (ICAR, New Delhi, India) in 2015. Dr. Qureshi was selected for the prestigious Raman Fellowship Programme for advanced post-doctoral research on “Marker Assisted Breeding for Quality Improvement in Dry Beans” at Michigan State University, USA for one year (2016–2017). He is also the recipient of INSA Summer Research Fellowship of Indian National Science Academy, Bengaluru and has handled five research projects from different funding agencies. He has published more than 60 research papers in journals of national and international repute. He is a member of many professional societies involved in crop improvement and was

associated as a breeder in the development and release of two oilseed brassica varieties, Shalimar Sarson-2 and Shalimar Sarson-3 (*B. rapa* var. brown sarson), and two rice varieties, Shalimar Rice-4 (low altitude) and Shalimar Rice-5 (high altitude).



Zahoor Ahmad Dar is Professor of Plant Breeding and is working as Principal Investigator in the AICRP (Maize) Srinagar Centre at DARS, Budgam, SKUAST-K and has been a gold medalist at his bachelor's and doctorate levels. He has published more than 200 Research papers in various international and national journals. He is involved in guiding various students at master's and doctorate levels. He has been involved in the development of 15 varieties in maize, oats, pulses, and brown sarson. He has handled nine projects from different funding agencies. He is the recipient of the INSA Summer Research and Visiting Scientist Fellowship. He has registered more than 75 germplasm accessions of maize with NBPGR and is a member of various societies at national and international levels involved in crop improvement. He has authored five books on plant breeding.



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several books on current topics in crop improvement for abiotic stress tolerance published by Springer Nature and CRC press USA. His Ph.D. research won first prize in the North Zone Competition, at national level, in India. He was awarded a Young Scientist Award from the Society for Promotion of Plant Sciences, Jaipur, India, in 2009. He is a fellow of the Society for Plant Research, India. Recently, he received the Young Scientist Award (Agriculture) 2015 from the Society for Plant Research, Meerut, India. He also served as visiting scientist in the Department of Plant Soil and Microbial Sciences, Michigan State University, USA, under the UGC-Raman Post-Doctoral Fellowship programme. He has attended several international and national conferences, presenting his research.

Chapter 1

Genomic Interventions for Biofortification of Food Crops



Abhishek Bohra, Uday Chand Jha, Rintu Jha, S. J. Satheesh Naik, Alok Kumar Maurya, and Prakash G. Patil

1.1 Introduction

Global food security covers not only the quantity of food but also the quality of food that is consumed. Nutrition is a cause of concern to confer good health to new world generation. Although a 27% decrease has been witnessed in the level of world hunger over the last seventeen years, millions of people still experience chronic hunger; this may be attributed to occurrence of famine due to changing climatic factors and geopolitical conflicts (<http://www.globalhungerindex.org/>). The situation where the food, deficient in vitamins and minerals, remains insufficient to meet the nutritional needs of the people is referred to as hidden-hunger or malnutrition. The prevalence of the malnutrition reflects from the fact that more than 30% of women of reproductive age worldwide suffer from anaemia, which also renders the children vulnerable from nutrition and health (WHO 2017). Equally importantly, world is still home for 154.8 million stunted and 52 million wasting children under five years of age group. Rural and semi-urban areas are more vulnerable to hidden-hunger. The intermittent crop failures and lack of other remunerative means to buy the increasing cost of healthy foods are the prime cause for increase in hunger and hidden-hunger. Deficiencies of iron (Fe), zinc (Zn) and/or other micronutrient are reported to plague more than two billion people worldwide (De Valença et al. 2017). Of the total deaths occurring among 6–60 months aged children in developing countries, a staggeringly high proportion (41%) is attributed to malnutrition (Schroeder and Brown 1994). The cereal-based food makes the dominant portion of the diets of the people suffering from micronutrient deficiency, especially in developing world.

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The growing problem of nutrient deficiency worldwide calls for implementing timely interventions at the community level. In the context, potential ways suggested to alleviate nutrient deficiencies include (1) Direct or nutrition-specific interventions that involve altering the consumption behaviour (dietary diversification, micronutrient supplementation, etc.) and (2) Indirect or nutritional-sensitive interventions or biofortification. Biofortification remains the most sustainable means for increasing the nutrient density of crop plants during plant growth through genetic or agronomic practices (De Valença et al. 2017; Bouis and Saltzman 2017). Biofortification offers a way to reach larger target population whereas supplementation and conventional fortification activities might be difficult to implement and/or limited. The genetic interventions facilitating biofortification include plant breeding protocols and transgenic techniques or genetic engineering. In this chapter, we cover crop biofortification using breeding techniques, a process that involves assessment of genetic variation for mineral nutrients in crop's gene pool, understanding the genetic architecture of the nutrient trait, and eventually the introgression of the genes responsible for greater nutrient density to deliver nutrient-rich crop cultivars. The immense potential of the large-scale elemental profiling techniques or ionomics and modern breeding methods like genomic selection (GS) is also discussed in relation to biofortification breeding of food crops. Comprehensive reviews on nutritional enhancement of crops have been published in recent years (Dwivedi et al. 2012; Graham et al. 2001; Hirschi 2009; White and Broadley 2009). Therefore, we will be focusing on the latest findings on crop biofortification that have been reported over the last 5 years. More recently, Bouis and Saltzman (2017) reviewed the progress of biofortification witnessed during 2003–2016 with a focus on HarvestPlus programme.

1.2 Genetic Variation for Various Micronutrients in Crop Plants

Crop genetic resources particularly landraces and wild relatives serve as reservoir of natural variation for improving breeding traits including mineral concentration. Genetic variability for mineral content has been evident in various crop species from various studies. Examples include grain Zn showing variation up to 11.6-fold among various cereal crops (Bänziger and Long 2000; Gregorio et al. 2000) and 6.6-fold in grain legumes (Raboy et al. 1984). Adequate genetic variation for grain Zn was recorded in rice following survey of 1763 accessions under multiple water regimes (Pinson et al. 2015). The variation ranged from 15.72 to 65.01 mg/g under flooded condition, whereas the range under non-flooded regime was noted to be 19.34–63.13 mg/g. Additionally, concerning grain Fe content, sufficient genetic variability was noted in this large panel of rice accessions, with variation ranging from 1.55 to 16.58 mg/g (under flooded condition), and 0.09 to 25.89 mg/g (under non-flooded condition). Importantly, various rice genotypes such as Nagina 22,

Honduras, Jeerigesanna, Kalabath, Pusa Basmati (Mahender et al. 2016) were identified as potential sources for increasing grain Zn content. In case of basmati rice, Zn content was found to be varying between 25 and 165 µg/g, whereas Fe content varied from 32 to 218 µg/g (Renuka et al. 2016). Additionally, the authors also examined the aromatic rice lines for grain β-carotene, revealing significant variation in β-carotene ranging from 1.23 to 9.9 µg/g in brown rice, and 0.08–1.99 µg/g in milled rice. Trijatmiko et al. (2016) reported up to 16 µg/g grain Zn content in high yielding elite polished rice. Moreover, to mitigate the challenge of Zn deficiency in human population worldwide, “Harvest Plus” breeding programmes have set the target of increasing Zn up to 28 µg/g in biofortified rice (Trijatmiko et al. 2016).

In wheat, Zhao et al. (2009) reported up to 2.6-fold variation for grain Zn content, ranging from 13.5 to 34.5 mg/kg. Apart from cultivated hexaploid wheat, wild emmer, einkorn, and landraces (Cakmak et al. 2000; Ortiz-Monasterio et al. 2007) and *T. dicoccoides*, *Ae. tauschii*, *T. monococcum* (Cakmak et al. 2000) act as natural storehouse for improving grain Zn content in wheat. Similarly, substantial amount of genetic variability was reported in spring and winter wheat ranging from 20 to 39 mg/kg and spring wheat possesses higher grain Zn than the winter wheat (Morgounov et al. 2007). Additionally, the authors also examined the genetic variation for grain Fe content that ranged from 25 to 56 mg/kg. With high concentration of Zn (up to 70 kg/mg) and Fe (up to 70 kg/mg) in grain, spelt wheat was identified as potential source for improving mineral traits in the crop (Gomez-Becerra et al. 2011). Another study in wheat uncovered substantial genetic variability for grain Zn concentration (7.4–59.4 mg/kg) from a larger set of diverse genotypes (Pandey et al. 2016). More recently, Manickavelu et al. (2017) surveyed variation of grain Zn content among 269 Afghan wheat landraces, and the authors found grain Zn varying from 15.56 to 87.29 ppm.

In maize, significant amount of genetic variation for grain Zn concentration (5.41–30.85 mg/kg) was recorded in 50 genotypes grown across various agro-climatic zones in India (Mallikarjuna et al. 2015). Similarly, in sorghum, Jambunathan (1980) observed considerable range of grain Zn (1.10–5.02 mg/100 g) and grain Fe content (3–11.30 mg/100 g). Badigannavar et al. (2016) also observed wide variation in grain Zn content (1.12–7.58 mg/100 g) in sorghum. More recently, after testing 336 individuals derived from the cross 296B × PVK801 under multi-location trials, the range of genotypic variation for grain Zn content was found to be 10.2–58.7 mg/kg in sorghum (Phuke et al. 2017).

Millet crops remain instrumental in offering essential micronutrients to human foods basket. Pearl millet, an important member of millet crop family, demonstrates significant genetic variation ranging from 25 to 65 mg/kg (Velu et al. 2007). Additionally, A wide range for grain Zn was noted from 319 diverse genotypes ranging from 10 to 86 µg/g and the two genotypes GEC164 and GEC543 showed higher accumulation of grain Zn (Yamunarani et al. 2016).

Several potential donors viz., Annada, ASD 16, CH 45, HKR 126, Nagina 22 and wild relatives such as *Oryza nivara* and *O. rufipogon* (see Anuradha et al. 2012) have been reported in rice for improving grain Fe content. Significant genetic

variation (from 0.25 to 34.8 $\mu\text{g/g}$) was also found for grain Fe content in rice landraces, with Swetonunia showing the highest Fe content of 34.8 $\mu\text{g/g}$ (Roy and Sharma 2014). Zhao et al. (2009) recorded a 1.8-fold genetic variation for grain Fe content in wheat. Wild emmer wheat showed high variability for grain Fe content (Gomez-Becerra et al. 2010) followed by durum wheat (Velu et al. 2011). Importantly, spring wheat possesses higher concentration of grain Fe than winter wheat (Liu et al. 2014). Examination of a large set of Indian and Turkish genotypes revealed wide variation in grain Fe content from 9.2 to 49.7 mg/kg. Significant amount of genetic variability varying from 55.14 to 122.2 ppm has been registered in a large set of 269 Afghan wheat landraces (Kondou et al. 2016; Manickavelu et al. 2017).

Higher grain Fe content extending up to 9.54 mg/100 g has been suggested in sorghum (Badigannavar et al. 2016). In addition, grain protein content varying from 3.50% to 12.60% became evident from 112 landraces and varieties assessed from this study. In sorghum, Phuke et al. (2017) reported significant genetic variability for grain Fe content ranging from 10.8 to 76.4 mg/kg conducting trails in various locations and different years. Likewise, large variation for grain Fe content varying from 18.88 to 47.65 mg/kg reflected from analysis of 50 diverse maize genotypes grown across various locations in India (Mallikarjuna et al. 2015).

Selenium is an important micronutrient for combating various diseases in human (Adams et al. 2002). A daily uptake of 55–200 μg of Se is beneficial for human health (Monsen 2000). Wheat also serves an important source of Se for combating Se deficiency in human (Guerrero et al. 2014; Eiche et al. 2015). Poblaciones et al. (2014) suggested that the accumulation of Se in wheat grain is up to 5.53 mg/kg. High variability of grain Se content reaching up to 7.2-fold (33–238 mg/kg) has been reported in wheat (Zhao et al. 2009). Among grain legume crops, lentil is an important source of Se content ranging from 166 to 858 $\mu\text{g/kg}$ apart from carrying high protein (Ates et al. 2016). Earlier, Rahman et al. (2013) also demonstrated wide variation in seed Se content of lentil, ranging from 74 to 965 $\mu\text{g/kg}$.

Grain protein content in rice remains low (8.5%) in comparison to wheat (12.3%), barley (12.8%) and millets (13.4%) (Mahender et al. 2016). On the basis of dry weight, Mohanty et al. (2011) reported 16.41% crude protein in ARC 10063 rice genotype and 15.27% crude protein in ARC 10075 rice genotype. In case of wheat existence of significant genetic variability for grain protein has been assessed (Peleg et al. 2008; Amiri et al. 2015). Grain protein ranging from 10.1% to 17.1% has been assessed in diverse wheat genotypes collected from India and Turkey (Pandey et al. 2016). Likewise, substantial amount of genetic variability for grain protein ranging from 10.9% to 13.6% was predominantly higher in bicolor-guinea race (Rhodes et al. 2017).

Significant genetic variation for grain Mn content was found under both flooded (14.35–46.51 mg/g) and unflooded (15.37–76.00 mg/g) conditions in rice (Pinson et al. 2015). In wheat also, ample genetic variability for grain Mn was recorded that ranged from 5.82 to 66.5 mg/kg (Khokhar et al. 2018).

β -carotene precursor of pro-vitamin A remains an important micronutrient for human health for ameliorating vitamin A deficiency in world human population (Giuliano 2017). Among cereals, rice, wheat and maize harbour a certain amount of genetic variability for grain carotene content (Zhai et al. 2016). In case of wheat, variability for β -carotenes at endosperm level has been investigated by different research groups (Qin et al. 2012; Qin et al. 2016). Similarly, preponderance of β -carotene in maize has been examined by various researchers (Harjes et al. 2008; Yan et al. 2010). Considerable zeaxanthin (1.2–13.2 $\mu\text{g/g}$ dry weight), β -cryptoxanthin (1.3–8.8 $\mu\text{g/g}$ DW) and β -carotene (1.3–8.0 $\mu\text{g/g}$ DW) in maize has been suggested (Muzhingi et al. 2017). In chickpea, the total carotenoid content ranged from 22 $\mu\text{g/g}$ (yellow cotyledon kabuli type) to 44 $\mu\text{g/g}$ (green cotyledon desi type) at post-anthesis stage (Rezaei et al. 2016).

1.3 The Genetic Structure of Mineral/Nutrient Content in Crop Plants

1.3.1 Discovery of QTL Controlling Micronutrient Content in Crops

Understanding the genetic nature of grain micronutrient has been met with limited success, and this may be attributed to complex quantitative inheritance of this trait coupled with substantial influence of genotype \times environment (G \times E) interactions upon elemental concentration (Mahender et al. 2016). Low to moderate estimates of heritability underlying nutrient (in particular, minor elements) content in plants adds to poor understanding of its genetic nature (Manickavelu et al. 2017). Given this, finding genomic regions or QTL that explain substantial phenotypic variation is key to elucidate the genetic basis of various traits controlled by several gene(s) including grain micronutrient content. Several studies in different crops, particularly in cereals and grain legumes, have reported QTL for micronutrient content viz., for grain Zn (Zhou et al. 2010; Qin et al. 2012), Fe (Lung'aho et al. 2011), Mn (Zhou et al. 2010; Zhang et al. 2014), protein (Blanco et al. 2006), β -carotene (Kandianis et al. 2013; Jittham et al. 2017) contents and so forth.

In rice, several QTLs controlling grain Zn have been reported (Garcia-Oliveira et al. 2009; Zhang et al. 2014; Swamy et al. 2016). Readers are referred to recent literature for greater details (Bohra et al. 2015, 2016). Ishikawa et al. (2017) identified a total of 4 QTLs controlling grain Zn on LGs 2, 9 and 10 from a back-cross recombinant inbred population (*O. sativa* 'Nipponbare' \times *O. meridionalis* W1627) (see Table 1.1). A more recent study on fine mapping of *qGZn9* QTL revealed two tightly linked loci (*qGZn9a* and *qGZn9b*) and the study led to pinpointing a candidate gene *Os09g0384900*. Similarly, in wheat, various genomic regions associated with grain Zn and Fe content were detected on various chromosomes through QTL

Table 1.1 List of QTLs controlling various micronutrients in crop plants

Crop	Nutrient element	Mapping population	QTL/loci/genomic region	Type of marker	LG/chromosome no.	PV%	Reference
Rice	Zn	<i>O. sativa</i> 'Nipponbare' × <i>O. meridionalis</i> W1627, BIL (151)	<i>qGZn2-1</i> and <i>qGZn2-2</i> <i>qGZn9</i> , <i>qGZn10</i>	<i>RM24085-RM566</i> <i>RM171-RM590</i> <i>RM573</i> , <i>RM6</i>	2, 9, 10	15–21.9	Ishikawa et al. (2017)
Rice	Mn	93-11 × PA64s RIL (132), CSSL	A major QTL <i>qGMN7.1</i>	SNP7-53 and SNP7-64 RM427 and RM11	7	15.6–22.8	Liu et al. (2017)
Maize	Zn and Fe		A total of 22 QTLs	SSR	1, 2, 3, 4, 5, 6, 7, 8, 9 and 12	–	Jin et al. (2015)
Wheat	Zn	<i>Triticum spelta</i> L. × synthetic hexaploid	<i>QGZn.cimmyt-7B_IP2</i>	DArT	7B	10.3–32.7	Crespo-Herrera et al. (2017)
	Fe	RIL (188) <i>Triticum spelta</i> L. × synthetic hexaploid RIL (188)	<i>QGZn.cimmyt-7B_PI</i> <i>QGFe.cimmyt-4A_P2</i> <i>QFe.cimmyt-3A_PI</i>		4A		
Wheat	Zn	Saricanak98 × MMS/4 (RIL) Adana99 × 70,711 (RIL)	2QTLs	DArT	1B and 6B 6A and 6B		Velu et al. (2016a, b)
Wheat	Fe, Zn	'Berikut' × 'Krichauff', BC	2 QTLs for Zn and one QTL for Fe	gwm120-wp/2430 wmc036-cfa2129	1B and 2B	22.2–35.9	Tiwari et al. (2016)
Wheat	Fe, Zn	WH542 × synthetic derivative	<i>QGFe.iari-2A</i> , <i>QGFe.iari-5A</i> <i>QGFe.iari-7A</i> , <i>QGFe.iari-7B</i> <i>QGZn.iari-2A</i> , <i>QGZn.iari-4A</i> , <i>QGZn.iari-2A</i> , <i>QGZn.iari-4A</i> <i>QGZn.iari-7B</i>	SSR	2A, 5A, 7A, 7B	20 32	Krishnappa et al. (2017)

Wheat	Fe, Zn	Seri M82 × SHW CWI76364	One major QTL	–	4BS	19.6	Crespo-Herrera et al. (2016)
Wheat	Protein	Yumechikara × Kitahonami DH (94)	<i>QGpc.2B-yume</i>	SSR, Xgpw4382	2B	32.1	Terasawa et al. (2016)
Wheat	Se	Tainong 18 × Linmai6, RIL	16 QTLs	D-3033829 and D-1668160	1B, 2B, 4B, 5A, 5B 5D, 6A, and 7D	7.71–20.22	Wang et al. (2017)
Maize	Fe, Zn, Mn	RIL	–	–	–	–	Zhang et al. (2017a)
Maize	Zn and Fe	Ye478 × Wu312, RIL (2012)	<i>qMnCC1-1</i> , <i>qMnCC1-2</i> <i>MnCC2-1</i> , <i>qMnCC2-1</i> <i>MnCC4-1</i> , <i>qMnCC4-2</i> <i>qZnCT4-1</i> , <i>qZnCT4-2</i> <i>qZnCC5-1</i> , <i>qZnCC5-1</i>	SSR	–	6.22–27.7	Gu et al. (2015)
Maize	Zn and Fe	–	mMQTL2.1, mMQTL3, mMQTL5 mMQTL9.2	SSR	2, 3, 5 and 9	–	Jin et al. (2015)
Maize	β-carotene	By804 × B73, RIL (178)	A total of 62 QTLs	SSR, SNP, InDel	1–10.	4.21–47.53	Jittham et al. (2017)
Sorghum	Protein	–	Alpha-amylase 3 gene	SNP	2	–	Rhodes et al. (2017)
Sorghum	Protein	(BTx642 × BTxARG-1) RIL (BTxARG-1/P850029) RIL	One QTL	SNP	1 and 2	–	Boyles et al. (2017)
Soybean	Protein	Nannong94–156 × Bogao RIL(152)	32 QTLs for water soluble protein content and grain protein content	SNP	3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 18, 19 and 20	2–29.2	Zhang et al. (2017b)
Pearl millet	Zn and Fe	130 accessions	16 significant MTAs for Zn and Fe	SSRs, <i>Xpsmp</i> 2261 <i>Xipes</i> 0180 <i>Xipes</i> 0096	3, 4, 5, and 7	11.3–13.4	Anuradha et al. (2017)

(continued)

Table 1.1 (continued)

Crop	Nutrient element	Mapping population	QTL/loci/genomic region	Type of marker	LG/chromosome no.	PV%	Reference
Pearl millet	Fe and Zn	841-P3 × 863B-P2 RIL (106)	2 QTLs for Zn and Fe on Same genomic region	DArT	3, 5, 7	42	Kumar et al. (2016)
<i>Brassica napus</i>	Protein	KenC-8 × N53-2	68 QTLs	SNP	A02, A03, A04, A07, A09 C01, C03, C05, C06 C07, C08 and C09	27.5	Chao et al. (2017)
Chickpea	Fe and Zn	ICC4958 × ICC 8261, RIL (277)	QTL (<i>CaqFe1.1</i> , <i>CaqZn2.1</i>) <i>CaqFe3.1</i> <i>CaqZn3.1</i> <i>CaqFZ4.1</i> <i>CaqFe4.1</i> <i>CaqFZ5.1</i> <i>CaqFZ7.1</i>	SNP	1, 2, 3, 4, 5 and 7	18.7–21.8 1.1–23.4	Upadhyaya et al. (2016a)
Chickpea	Protein	ICC 12299 × ICC 4958, RIL (F7)	Seven genomic region	SNP	1, 2, 4, 6 and 7	10–20.	Upadhyaya et al. (2016b)
Chickpea	Protein		19 significant MTAs/5QTLs	SSR	1, 2, 3, 4 and 5	8.64–16.85	Jadhav et al. (2015)
Common bean	Mn	DOR364 × G19833, RIL	3 QTLs		1, 5, 8		Blair et al. (2016)
Lentil	Fe and Zn	138 accessions	Two significant MTA for Fe One significant MTA for Zn	SNP	–	9–21.	Khazaei et al. (2017)
Lentil	Fe and Zn	96 accessions	4 significant MTA for Fe 4 significant MTA for Zn	SSR	–	9–11. 14–21.	Singh et al. (2017a)
Lentil	Se	PI 320937" × "Eston," RIL (96)	<i>SeQTL2.1</i> , <i>SeQTL5.2</i> <i>SeQTL5.3</i> and <i>SeQTL5.1</i>	SSR, SNP	2 and 5	6.3–16.9	Ates et al. (2016)

mapping experiments (Krishnappa et al. 2017; Srinivasa et al. 2014; Velu et al. 2016a, b). Crespo-Herrera et al. (2016) discovered recently a QTL *QGZn.cimmyt-7B_1P2* governing 32.7% of the phenotypic variation (PV) for grain Zn on chromosome 7B in wheat. Another QTL (*QGFe.cimmyt-4A_P2*) in wheat on chromosome 4A explained more than 20% PV for grain Fe content (Crespo-Herrera et al. 2017). Additionally, two major QTLs associated with grain Zn content could be located on chromosomes 1B and 6B from two recombinant inbred populations (Velu et al. 2016a). Importantly, one QTL on chromosome 2B controlling grain Fe content coincided with the genomic region harbouring QTL for grain Zn content. In a recent study in wheat, four QTLs (*QGFe.iari-2A*, *QGFe.iari-5A*, *QGFe.iari-7A* and *QGFe.iari-7B*) for grain Fe content with PV up to 20% PV and five QTLs for grain Zn accounting for 32% PV were reported by Krishnappa et al. (2017).

Several QTLs have been mapped on rice chromosomes 3, 7 and 8 for grain Mn concentration. Liu et al. (2017) found a major QTL, *qGMN7.1* explaining up to 23% PV for Mn concentration on LG 7 with a RIL population derived from 93-11 and PA64s. Further fine mapping of this QTL region uncovered a set of five genes *LOC_Os07g15350*, *LOC_Os07g15360*, *LOC_Os07g15390*, *LOC_Os07g15400* and *LOC_Os07g15370* within the target region of 49.3 kb. Subsequently, *LOC_Os07g15370* (*OsNRAMP5*) could be declared as the likely gene causing higher grain Mn accumulation (Liu et al. 2017). The authors also validated the findings using CSSL in the background of 93-11 containing *qGMN7.1* from PA64s. In wheat, a total of 16 QTLs contributing Se content at various stages viz., seedling, shoot and grain were discovered by Wang et al. (2017). Earlier, Pu et al. (2014) also reported five QTLs governing Se content in wheat.

Like cereal crops, grain legumes also remain important from the food security point due to higher content of protein and essential minerals. Analyses of mapping populations have provided a number of QTLs controlling mineral content in grain legumes (see Bohra et al. 2015). Ates et al. (2016) analysed the Se content in a RIL population developed from PI 320937 and Eston in lentil. The authors reported four QTLs, one on LG 2 and three on LG 5, with 16.9% being the highest PV explained by these QTLs. A non-exhaustive list of the QTLs available from latest studies is presented in Table 1.1.

1.3.2 Association Genetics to Discern Genomic Regions Linked with Mineral Traits

The ability of genome-wide association study (GWAS) to genetically dissect the trait-of-interest in a diverse panel (non-requirement of an artificially created population) with enhanced resolution makes this technique promising for associating nutrient content variation with genetic variants in crop plants (Diapari et al. 2014; Huang et al. 2015; Nawaz et al. 2015; Suwarno et al. 2015). A recent GWAS conducted on 378 brown rice accessions led authors to associate 20 QTLs with the

variation in concentrations of five mineral elements, i.e. Fe, Zn, Se, Cd and Pb (Huang et al. 2015). More importantly, QTL colocalizations observed on chromosomes 5, 7 and 11 hold great potential in relation to biofortification breeding in rice.

In a similar manner, genetic basis of eight essential grain mineral contents was examined in USDA minicore collection of brown rice with GWAS, which enabled identification of 37 genomic regions controlling accumulation of minerals like Zn, Fe, Mn, Mg, K, etc. (Nawaz et al. 2015). In wheat, marker-trait association analysis (MTA) in 47 synthetic lines facilitated discovery of six QTLs, three each for grain Zn and Fe (Gorafi et al. 2016). Recently, a GWAS in a collection of 336 spring barley line for content of various minerals led identification of 11 QTLs for grain Fe content, 3 QTLs for grain Zn and 3 QTLs for grain Mn (Gyawali et al. 2017). In chickpea, association mapping in a set of 94 diverse genotypes suggested significant association of 8 markers with variation in contents of Zn and Fe, and the MTAs were detected on LGs 1, 4, 6 and 7. Concerning protein content, a total of 19 MTAs explaining variation for seed protein content were detected in chickpea on different five chromosomes following an association study involving 187 accessions (Jadhav et al. 2015). Upadhyaya et al. (2016b) performed GWAS in 336 chickpea genotypes using 16,376 SNP markers and reported seven significant MTAs for seed protein content explaining up to 41% PV. The authors also validated five genes in the parental lines and the derived RILs.

In sorghum, significant MTAs were detected for grain protein content on chromosome 2 and 4 based on a genome-wide scan of a global set of 265 lines (Rhodes et al. 2017). In a previous study, Owens et al. (2014) deciphered the role of carotenoid biosynthesis candidate gene in maize through GWAS. Similarly, in maize, screening of a large panel of 380 lines for genome-wide associations led authors to discover seven significant MTAs for β -carotene (βC) on LGs 1, 2, 8 and 10, with PV up to 16% (Suwarno et al. 2015). Additionally, significant MTAs were obtained for β -cryptoxanthin (βCX : 13 MTAs) and zeaxanthin (ZEA: 14 MTAs). A more recent association analysis in 233 tetraploid wheat accessions using a high-density SNP array delineated a set of 24 candidate genes, which could be related to carotenoid synthesis (Colasunno et al. 2017).

1.4 Functional Genomics and Grain Micronutrients Accumulation in Crops

Unprecedented progress in plant functional genomics has shed new light on the candidate gene(s) and biosynthetic pathways associated with various complex traits including essential micronutrients of human importance. Several candidate gene(s) underlying grain Fe and Grain Zn content such as *OsYSL1*, *OsMTPI*, *OsNAS1*, *OsNAS3*, *OsNRAMP1*, heavy metal ion transporter, *OsAPRT* has been pinpointed in rice (Anuradha et al. 2012; Neelamraju et al. 2012). Based on association mapping and expression profiling, 16 genes involved in grain Fe and grain Zn accumulation

were found in chickpea (Upadhyaya et al. 2016a). Concerning seed protein content, six candidate genes encoding ATP-dependent RNA helicase DEAD-box, cystathionine-beta synthase, CMP and dCMP deaminases, G10 and zinc finger protein were reported in chickpea (Upadhyaya et al. 2016b). Following cloning of two carotenoid cleavage dioxygenase (CCD) genes viz. *CCD1* and *CCD4*, differential expression profiles of metabolic gene and homoeologs including *PSY1*, *LCYe*, *HYD1/2* and *CCD1/4* established in wheat offered important insights into β -carotene enrichment in the endosperm of wheat grains (Qin et al. 2016). Rezaei et al. (2016a) reported a total of 32 candidate genes in chickpea participating in carotenoid synthesis pathways and examined their expression pattern at various seed developmental stages in five chickpea genotypes.

In recent years, increasing attention is being paid towards discovery of non-coding (nc) RNAs engaged in regulating important traits such as grain micronutrient content in plants. Among the different classes of ncRNAs discovered in plants, micro RNAs (miRNAs) are endogenous small non-coding riboregulators with their lengths varying from 20 to 24 nucleotides (see Mishra and Bohra 2018). Paul et al. (2016) discovered participation of some known as well novel miRNAs in Fe translocation through analysing the small RNA sequencing libraries constructed from the roots of soy *FER1*-overexpressing transgenic rice. Importantly, *NRAMP4*, coding for a metal transporter, was predicted as a target gene for the novel miRNAs (miR11, miR26, miR30 and miR31). The authors proposed activation of *NRAMP4* as a result of the reduced expression of the above four novel miRNAs. The role of two genes *GRMZM2G366919* and *GRMZM2G178190* (members of *NRAMP* gene family) in grain Zn and Fe accumulation in maize was established through meta QTL analysis (Jin et al. 2015).

1.5 Transgenic Interventions for Enriching Grain Nutrient Content

Transgenic/genetic engineering (GE) is an alternative to conventional breeding enabling transfer of gene(s) across the species regardless of the sexual reproduction process. Improvement of grain micronutrient density through conventional breeding is greatly constrained by the limited variability for grain micronutrient available in the cultivated/crossable gene pool. In view of this, GE has been successfully employed for increasing micronutrients (Table 1.2), especially Zn, Fe, pro-vitamin A, etc. in grains of staple crops (Aluru et al. 2008; Abid et al. 2017; Boonyaves et al. 2017; Masuda et al. 2012). Transgenic approach has yielded notable results in different crops; for instance several fold increment in Fe content in rice endosperm (Bashir et al. 2013; Zhang et al. 2012; Ogo et al. 2011). Similarly, fourfold increase in grain Fe content and two-fold increase in transgenic rice overexpressing nicotianamine synthase (*OsNAS*) genes is noteworthy (Johnson et al. 2011; Wirth et al. 2009). Likewise, a transgenic rice event overexpressing *OsNAS2* and soybean

Table 1.2 List of transgenes contributing to higher micronutrients in various crop plants

Crop	Micronutrient	Source	Gene	Reference
Rice	Fe	Rice and barley	<i>OsYSL2</i> , <i>HvNAS1</i>	Masuda et al. (2012)
Rice (Pusa-sugandhi II)	Fe	Rice	<i>Ferritin</i>	Paul et al. (2012)
Rice	Fe	Arabidopsis	<i>AtIRT1</i> , <i>AtNAS1</i> , <i>PvFER</i>	Boonyaves et al. (2017)
Rice (IR64)	Fe	Soybean	<i>OsNAS2</i> , <i>SferH-1</i>	Trijatmiko et al. (2016)
Rice	Fe, Zn	Arabidopsis	<i>AtIRT1</i>	Boonyaves et al. (2016)
Rice (IR64)	Fe and Zn	Rice	<i>OsNAS</i>	Moreno-Moyano et al. (2016)
Rice (Nipponbare)	Vitamin A	Arabidopsis, Maize, Common bean	<i>AtNAS1</i> , <i>PvFERRITIN</i>	Singh et al. (2017b)
		Bacteria	<i>CRTI</i> , <i>ZmPSY</i>	
Rice (Tsukinohikari and Tachisugata)	Fe and Zn	Soybean	<i>FER 1</i>	Paul et al. (2016)
Rice	Fe	Yeast	<i>refre1/372and</i> <i>OsIRO2</i>	Masuda et al. (2017)
Maize	Vitamin A	Bacterial	<i>crtB</i> , <i>crtI</i>	Aluru et al. (2008)
Wheat	Fe and Zn	<i>Aspergillus japonicus</i>	<i>phyA</i>	Abid et al. (2017)

ferritin (*SferH-1*) genes showed dramatic increase in contents of grain Fe (up to 15 µg/g) and Zn (45.7 µg/g) in the field trials conducted in two countries (Trijatmiko et al. 2016). The study offered further evidences confirming the endosperm enriched with Fe and Zn, and the bioavailability of the Fe. Enhanced concentration of grain Fe was demonstrated both in polished and unpolished rice through transgene expression of *AtIRT1*, *AtNAS1* and *PvFER* genes (Boonyaves et al. 2017). A previous study by the same group showed up to 9.6 µg/g DW increase in grain Fe in the polished rice grains consequent upon the expression of *AtIRT1* gene in association with *AtNAS1* and *PvFERRITIN* genes (Boonyaves et al. 2016). Recently, Abid et al. (2017) attempted to overcome the limitation posed by phytate, a chelating agent reducing the bioavailability of micronutrient viz., Fe, Zn in various crops. Transgenic expression of *Aspergillus japonicus* phytase gene (*phyA*) in wheat endosperm allowed higher bioavailability of grain Fe and Zn in wheat through enhancing the activity of phytase enzyme.

1.6 High-Throughput Ionome Profiling and Biofortification Breeding

With tremendously improving genotyping/sequencing platforms, large-scale and accurate phenotyping assumes greater significance with respect to improving micronutrient content in different crops. In this context, ionomics has been emerging as high-throughput “elemental profiling” approach that surveys the mineral nutrient of a living organism (Huang and Salt 2016; Baxter 2009). Precise and accurate measurement of existing grain micronutrients accelerates the progress of identification of genetic lines carrying high micronutrient content (Swamy et al. 2016). Several non-destructive high-throughput elemental analytical techniques viz., Atomic Absorption Spectrometry (AAS), inductively coupled plasma mass-spectrometry (ICP-MS), inductively coupled plasma-optical emission spectrometry (ICP-OES), synchrotron X-ray fluorescence microscopy (XFM), energy dispersive X-ray fluorescence spectrometry (Trijatmiko et al. 2016; Manickavelu et al. 2017; Khokhar et al. 2018) have been employed to measure nutrient density in plants. To this end, some community-oriented platforms have also been established rendering the ionic data freely available to public. Examples include ionic HUB or iHUB (<http://www.ionomicshub.org/home/PiiMS>) that allows researchers to access ionic resources pertaining to Arabidopsis, rice, yeast and soybean (see Baxter et al. 2007). This international collaborative workspace supports tools enabling data annotation, data collection and workflow, and data sharing.

1.7 Whole-Genome Predictions for Improving Elemental Concentrations of Crops

Though the cost of genotyping is being reduced dramatically, the phenotyping bottlenecks still pose a big hurdle to crop breeding progress (see Bohra 2013). In such a scenario, new breeding methods like genomic selection (GS) holds great promise as GS accelerates selection cycles as well as selection gains per unit of time (<http://genomics.cimmyt.org/>). GS has been extensively used in livestock industry including sheep, dairy cattle, pig breeding, poultry (Meuwissen et al. 2016) and allowed selection of traits that are “hard-to-measure” and allowed increasing rate of genetic improvement in animal breeding programmes (van der Werf 2013).

In GS, prediction models are trained using a reference population or training set that is scored both genotypically and phenotypically (Meuwissen et al. 2016). Genomic estimated breeding values (GEBVs) are then calculated and based on these GEBVs selection is practiced in breeding population that is scored only at genotypic level, thus circumventing the need for costly and time-consuming phenotypic recordings. Lorenz et al. (2011) have described several methods that have been proposed to calculate genomic predictions such as random regression best linear unbiased prediction (RR-BLUP), least absolute shrinkage and selection