

EDITORIAL

Multi-faceted approaches for breeding nutrient-dense, disease-resistant, and climate-resilient crop varieties for food and nutritional security

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WHY BOTHER?

The world population will surpass nine billion by 2050; hence the yield of primary staple crops must increase to feed the growing world population (Tilman et al. 2011; Ray et al. 2013; Molotoks et al. 2021). Another challenge facing agriculture is increasing global temperature, which is expected to be 1.1 to 5.4 °C warmer by the end of this century (Tollefson 2020). Given these dire predictions, crops are expected to experience heat stress during their growing season and more frequent droughts (Mir et al. 2012; Zhao et al. 2017; Fahad et al. 2017; Rustgi et al. 2021). These changes would result in nutritional insecurity and instability owing to crop productivity decreases, specifically in the world's resource-deprived and most populated parts (Maja and Ayano 2021; Molotoks et al. 2021). Plant breeders are finding novel ways to meet this ever-increasing demand for food grains given the climatic atrocities such as increasing global temperatures, erratic rain patterns, and accompanying changes in pest and pathogen populations (White et al. 2011; Maja and Ayano 2021). Another layer of complexity is diminishing resources (land and water availability, soil health, and increasing production cost), the demand to reduce agriculture's carbon footprint, and adaptation of rentable practices to improve sustainably in agriculture. To meet these targets, plant breeders have developed improved cultivars of different crop plants largely by using conventional plant breeding approaches involving genetic crossing and selection for the desired traits, but this strategy primarily focused on the crop's primary gene pool (Kaiser et al. 2020). However, recent advances now mean that molecular plant breeding can include genomic and biotechnological approaches, offering plant breeders to introduce desired genetic changes in the crop genome from a wider gene pool with greater precision and speed. Therefore, the conventional crop improvement approaches are aggressively being supplemented by molecular plant breeding approaches to achieve the desired outcome in a relatively short duration (Hasan et al. 2021).

THE POSSIBLE SOLUTION!

The genomics revolution of the last two decades has resulted in the development of many different molecular marker types and genetic and physical maps. Indeed, this period also witnessed the evolution of many high-throughput and precise genotyping and phenotyping methods (Gupta and Rustgi 2004; Gupta et al.

2008, 2013a; Mir et al. 2013; Mir and Varshney 2013; Tyagi et al. 2019, 2021; Yang et al. 2020). Furthermore, it has led to the discovery of genes and trait-associated DNA markers, precisely via quantitative trait loci (QTL) mapping and genome/transcriptome-wide association analysis (Mir et al. 2012; Li et al. 2022a; Zhou et al. 2022). However, the tremendous progress made in genotyping methods has shifted the research bottleneck from whole-genome genotyping to the collection of phenotypic data. Therefore, despite some progress in this direction in the last decade, more concerted efforts are needed to complement the progress made in the plant genomics realm (Mir et al. 2015, 2019).

The recent advances in DNA sequencing technologies have also resulted in the discovery of a variety of polymorphism detection approaches such as whole-genome re-sequencing (WGR), restriction site-associated DNA (RAD) genotyping, and QTL sequencing (QTLseq), to name a few (Mir et al. 2013; Mir and Varshney 2013). These approaches are gaining popularity as primary genotyping methods for gene discovery in crop plants. The efficiency and precision of gene mapping, transfer, and stacking to develop nutrient-dense, pest- and pathogen-resistant, and climate-resilient cultivars are expected to be higher with these genomic tools and techniques. Another set of tools available to plant breeders is through recent advances in genetic transformation and methodological technologies; for example, the use of morphogenic genes (that trigger in vitro embryogenesis) to reduce genotype dependence and the advent of genome editing methods, which has increased the scope of plant breeding to tailor crops according to the specific needs (Zhan et al. 2021; Saurabh 2021). Such recent advances in methodologies and models will maximize the power to identify novel genes (Li et al. 2022a, b; Zhou et al. 2022). Although each of these approaches offers individual benefits, it is desirable to adopt a multi-faceted approach including the components of genomics/transcriptomics, proteomics, metabolomics, ionomics, phenomics, and genetic engineering to meet the needs of today and tomorrow (Scossa et al. 2021). Given this understanding, we planned a special issue of the journal *Heredity* focused on the 'Multi-faceted Approaches for Breeding Nutrient-Dense, Disease Resistant, and Climate Resilient Crop Varieties for Food and Nutritional Security'. The special issue includes 11 papers, comprising both original research and review articles. To provide an overview, a summary of the manuscripts included in this special issue is offered below.

DEVELOPMENT AND USE OF MOLECULAR MARKERS

Molecular markers are important genomic resources for crop improvement programs. Many different types of molecular markers are available and have been used to study genetic diversity, population structure, and marker-trait associations (c.f.

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Gupta and Rustgi 2004; Gupta et al. 2008; Mir and Varshney 2013; Tyagi et al. 2019, 2021; Sihag et al. 2021; Kumar et al. 2021). The manuscript by Sagwal et al. (2022) described the development of simple sequence repeat (SSR) markers from coding and non-coding RNA genes in common wheat and identified markers that showed association with Nitrogen and Phosphorus use efficiency. For this purpose, they evaluated a set of 98 SSRs, including 66 microRNA and 32 protein-coding genes, derived, on a panel of ten wheat genotypes (including N and P efficient and deficient lines). The screen yielded two SSRs, namely miR171a and miR167a, which can discriminate between genotypes with high and low N/P use efficiencies. After re-validation of the markers to discriminate between high and low N/P use efficiencies using different genotypes in future, these markers could be used as functional markers for wheat germplasm characterization for N and P use efficiencies.

GENE DISCOVERY THROUGH QTL MAPPING AND GENOME-WIDE ASSOCIATION STUDIES (GWAS)

Two important approaches, QTL interval mapping and association mapping, are available for discovery of genes/QTLs for quantitative traits (Gupta et al. 2013b; Li et al. 2022a; Zhou et al. 2022). While QTL mapping is now considered a more traditional approach, genome-wide association mapping is considered a somewhat more modern approach. Both these approaches have advantages and disadvantages (Mir et al. 2012) and have been used in almost all crop plants to discover genes for important target traits. He et al. (2022) discovered several important genes/QTLs for head blight resistance in common wheat. The study involved using two recombinant inbred line (RIL) populations derived from a genetic cross between wheat genotypes with contrasting head blight responses. For this study, the population was phenotyped across multiple locations and years in South America, Bangladesh, and Zambia. The study reported using high-throughput DArTseq[®] technology as a genotyping platform and identified genes/QTLs explaining 16.7 to 79.4% of the phenotypic variation across experiments, including one major consistently detected QTL on the 2NS/2AS translocation region in both populations. The 2NS/2AS translocation is considered a very important chromosomal translocation in bread wheat from *Triticum ventricosum* (sin. *Aegilops ventricosa*) and possesses a cluster of resistance genes for many important wheat diseases. Additionally, several minor genes/QTLs were also identified, which could be deployed in wheat breeding programs globally.

Another study by Singh et al. (2022) focused on the genetic dissection of days to flowering and leaf shape in pigeon pea using a bi-parental F₂ population. They used a high-throughput “QTL-seq” approach to identify candidate genes contributing to these traits. The authors identified nine single-nucleotide polymorphisms (SNPs) in seven candidate genes for days to flowering and 39 SNPs in 20 candidate genes for leaf shape. These findings were further validated through co-segregation analysis using the whole F₂ population via another important approach, genotyping-by-sequencing (GBS). The comparative analysis of seven identified genes for days to flowering was also conducted on 12 Fabaceae genomes, and conserved synteny was observed in nine genomes. The identified candidate gene(s) for days to flowering and leaf shape are expected to be used extensively in pigeon pea breeding programs.

The study by Fradgley et al. (2022) focused on the complex interaction of end-use performance and nutritional quality traits, precisely mineral density due to positive and negative interactions among traits with direct implications for wheat breeding. The authors investigated the correspondence between several milling and baking traits and mineral density in a multi-parent population over two trial years to determine whether the pleiotropic or linked QTLs control these traits. In this analysis, the co-location of major

QTLs and principal component-based multi-trait QTLs increased the power to detect QTL with pleiotropic effects, explaining many complementary and antagonistic trait relationships. In addition, some known genes showed pleiotropic effects with end-use performance and nutritional quality traits, such as: 1) high molecular weight glutenin subunit genes explaining variation in dough rheology traits; 2) the *TaGW2* gene explaining variation in grain size and increased flour extraction rate; 3) the *Rht-D1b* gene exhibiting a positive effect on Hagberg falling number (a measure of α -amylase activity; a high Hagberg falling number indicates low α -amylase activity and good baking property) but a negative effect on grain size, specific grain weight, grain protein content and flour water absorption. Moreover, mineral nutrient content was lower in *Rht-D1b* lines. However, the potassium concentration was higher in these lines. Similarly, the presence of an awned spike showed an increase in calcium content and grain density without decreasing the flour extraction rate. Collectively, this study demonstrated the utility of marker-assisted selection in optimizing trait interactions and enhancing wheat nutritional quality while retaining end-use performance.

Association mapping is another important approach being used for the genetic dissection of quantitative traits in crop plants and offers several advantages over the conventional QTL mapping approach involving bi-parental populations. Vikas et al. (2022) undertook a GWAS for the genetic dissection of leaf rust resistance in common wheat. A multi-locus-GWAS was performed to identify quantitative trait nucleotides (QTNs) or genomic regions associated with seedling- and adult-plant leaf rust resistance. The study used a panel of 400 diverse wheat genotypes that were assayed for 35 K SNPs. This analysis identified 51 QTNs for seedling resistance and 15 QTNs for adult plant resistance (APR). The SNPs associated with the trait of interest in at least two GWAS models were considered reliable QTNs. A set of three genomic regions were found to show association with seedling resistances to two/three-leaf rust pathotypes. The QTNs identified in this study can prove beneficial in wheat molecular breeding programs aimed at developing leaf rust-resistant varieties.

GENOMICS, REVERSE GENETICS FOR BREEDING CLIMATE-RESILIENT AND NUTRIENT-DENSE CROPS

Continued development of high-yielding crop plants that can thrive under changing climatic conditions is needed to assure food security in the coming decades. Maintaining a high yield under unfavorable climatic conditions requires the successful and uniform establishment of crop plants. A comprehensive review by Reed et al. (2022) focused on a complex quantitative trait, seed vigor, that includes seed longevity, germination speed, seedling growth, and early stress tolerance. It is a trait that is important for the establishment of a uniform crop stand early during the growing season to mitigate the effects of heat/drought stress. Also, it is known that an abrupt temperature fluctuation (elevated temperature) during the early stages of seed development can reduce seed size, number, fertility, and germination and reduce seed vigor in cereals, legumes, and vegetable crops. The review article discussed the recent advances in the genetic underpinnings of seed performance and how changing climate affects the seed vigor in cereals, legumes, and vegetable crops.

Husaini (2022) discussed how crop plants have to face multiple biotic and abiotic stresses simultaneously and discussed the complex quantitative nature of these stresses. The author emphasized using multi-function pleiotropic genes for imparting tolerance against multiple environmental stresses simultaneously. In addition, valuable information about abiotic stress (drought, salinity, submergence, cold, freezing, and heat) tolerance was also mined, and the role of high-value genes for breeding nutrient-dense weather-resilient crops was highlighted. The information

presented will prove useful for biotechnologists and breeders to develop better crops for the 21st century.

Kumar et al. (2022a) presented a detailed review on reverse genetic approaches for breeding nutrient-rich and climate-resilient cereals and food legumes. The article provides information on different reverse genetic approaches being used in the functional characterization of unknown genes, with an intent to use the information in breeding programs. A few examples elaborated in the review are abiotic stress-responsive genes and genes controlling agro-morphological traits. Under the heading 'Exploitation of reverse genetic-based functionally characterized genes in breeding,' the authors elaborated on the development of functional markers for accelerating genetic gain through marker-assisted or transgenic breeding using reverse genetics-based functionally characterized genes. Finally, the authors discussed the prospects of this technology alone or in combination with other technologies in addressing the projected food demands of the growing human population under changing climatic conditions in developing climate-resilient and nutrient-rich cultivars of cereals and legumes.

Among the different stresses affecting crop production and productivity, salinity stress is one of the most important atrocities that adversely affects plant growth and causes considerable losses in cereal crops. Like other stresses, salinity stress tolerance is also a complex phenomenon. The review article by Kumar et al. (2022b) highlighted the impact of salinity and elaborated on the key mechanisms/pathways for imparting salinity tolerance. Additionally, they summarized recent progress in mapping and introgressing major genes/QTLs; provided success stories of implementing genomics-assisted breeding, transcriptomics, proteomics, and metabolomics approaches in major cereals, such as rice, wheat, and maize for improving salinity tolerance; and finally discussed some future perspectives.

STATISTICAL GENOMICS TOOLS FOR MODERN PLANT BREEDING

The study by Meher et al. (2022) enhances our understanding of the choice of the selection method for genomic prediction in different crop breeding programs. Using commonly used genomic prediction models, the authors comprehensively evaluated the accuracy and bias of predicting genomic estimated breeding value (GEBV). The best linear unbiased prediction (BLUP) models were found effective for traits governed by many QTLs, with each exhibiting a minor effect on the genetic variance. On the contrary, Bayesian models outperformed BLUP for traits controlled by a few causal variants with larger effects. Furthermore, the BLUP methods were observed to be less biased for the prediction of GEBV, irrespective of the genetic architecture of the trait. This study would help choose an appropriate model for genomic prediction in different breeding programs.

GENOMICS-ASSISTED BREEDING (GAB)

One of the primary objectives in 21st century plant breeding is to improve the yield of the major staple cereals, i.e., wheat, rice, and maize. The study by Kaur et al. (2022) used a Marker-assisted Selection (MAS) approach to improve bread-making quality in a commonly used translocation of the short arm of chromosome 1 from rye (1R) into wheat chromosome 1B (1BL.1RS), which improves yield and resistance traits but compromises critical baking traits. The study involved the replacement of two important loci on the 1RS arm through MAS, which substantially improved the target bread-making traits in 30 promising advanced breeding lines, while retaining the advantage in yield and disease resistance traits offered by the translocation.

PERSPECTIVE

The papers published in this special issue have compiled a vast amount of knowledge on molecular plant breeding and advanced our understanding. The continuous evolution of genomics tools, techniques, and statistical methods is vital for advancing the discipline and breeding genotypes needed to meet future food, feed, and fiber demands. The advancements in developing new marker types, including miRNA-derived SSRs, are critical for studying the genetic relationships, population structure analysis, and marker-trait associations. Other vital emerging marker types include structural variations (SVs) and k-mers (a k-mer represents a sub-sequence of a certain length in any sequence in the genome), which will be used for genome-wide association studies (GWAS). In addition, recent advances in next-generation sequencing (NGS) technology have facilitated the development and use of pangenomes that will further add to the repertoire of DNA markers available for GWAS. These marker resources will help utilize the untapped genetic resources to precisely breed for the trait of interest in a short duration that was otherwise difficult to achieve.

Several articles in the special issue highlighted the use of high-throughput genotyping platforms for whole-genome scanning and mapping genes/QTLs for essential traits like biotic and abiotic stress tolerance, climate resilience, end-use quality, and nutrition. Important genetics resources like bi-parental mapping populations for QTL/gene discovery and diverse germplasm resources for genome-wide association studies (GWAS) have been used. However, the need of the hour is to develop multi-parental mapping populations to assure the detection power of the bi-parental populations and the precision of diverse populations in gene/QTL detection. In addition, new advanced gene discovery methods/multi-locus approaches need to be used to identify quantitative trait nucleotides (QTNs) that lead to the discovery of candidate genes for subsequent functional characterization via gene knockout, mutagenesis, and genome editing. The special issue offers examples of the use of multi-parental populations and also QTN identification and encourages the readers to utilize this knowledge in breeding nutrient-dense, disease-resistant, and climate-resilient crop varieties for food and nutritional security.

Reyazul Rouf Mir¹✉, Sachin Rustgi², Yuan-Ming Zhang³ and Chenwu Xu⁴

¹Division of Genetics & Plant Breeding, Faculty of Agriculture (FoA), SKUAST-Kashmir, Wadura Campus, Sopore, Kashmir, Jammu and Kashmir 193201, India. ²Department of Plant and Environmental Sciences, School of Health Research, Clemson University Pee Dee Research and Education Centre, Florence, SC 29506, USA. ³College of Plant Science and Technology, Huazhong Agricultural University, Wuhan 430070, China. ⁴College of Agriculture, Yangzhou University, Yangzhou 225009 Jiangsu, China. ✉email: imrouf2006@gmail.com

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RRM prepared the first draft and SR, Y-MZ, and CX read and corrected the draft.

COMPETING INTERESTS

The authors declare no competing interests.

ADDITIONAL INFORMATION

Correspondence and requests for materials should be addressed to Reyazul Rouf Mir.

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