EDITORIAL

Crop genetics research in Asia: improving food security and nutrition

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Breakthroughs in genomics research in recent decades have fundamentally changed the landscape of crop science at a number of fronts:

(1) High-quality reference genome sequences have become available for most of the crops which have provided the foundation for understanding the genome and for functional genomic studies.

(2) Large numbers of genes have been identified and functionally characterized for many important agronomic traits, which have greatly enhanced the understanding of the regulatory mechanisms and the underlying biological processes for the making of the traits.

(3) Large-scale resequencing of the diverse germplasms and genome-wide association studies (GWAS) have provided assessment about the extent of genome diversity, the genetic architecture, and association between the phenotype and DNA sequence polymorphisms in many crop species.

(4) Systems of breeding technologies based on the advance in genomic studies, or genomic breeding, have now been developed including novel goals in response to the evolving demands of the consumers, upgraded definitions of traits to be improved, techniques for whole genome selection, and varietal designs for the implementation.

Asia is the most populous continent and has been undergoing the most rapid economic growth among all the continents of the world. Food security and nutrition demands are highly pressing in all Asian countries. Asia is also the home for a large number of crops, including the most important food crops such as rice, wheat, barley, and chickpea and pigeonpea which were domesticated here. Accordingly, the scope and team of crop science research in Asia collectively are the largest among all continents. Research programs in a number of Asian countries have made great progress in many fields of diverse crops, which have greatly helped address the issues of food security and nutrition.

In this special issue, we invited a number of experts from several Asian countries to present the advances in various aspects of crop genetics research and also to offer their perspectives for future developments in a number of important food crops in Asia. There are 27 papers published in this issue covering rice, maize, wheat, barley, buckwheat, several legumes like soybean, groundnut, chickpea, and pigeonpea as well as vegetables, which are vital to the livelihood of Asian people. Here, we summarize some of the highlights of these papers.

Rice, a crop originated in Asia, provides the largest portion of calorie intake in most Asian countries. In the past two decades, rice has demonstrated to be a superb monocotyledon model for genomics and plant science research in a number of perspectives. This issue includes six rice papers.

There has been rapid progress in the studies of the epigenome in rice, which has greatly advanced our understanding of epigenetics in plants and the findings are comparable in many ways to the dicot model Arabidopsis. In the paper entitled Understanding epigenomics based on the rice model, Lu et al. (2020) provided a comprehensive overview of the recent researches on rice epigenomics, including DNA methylation, histone modifications, non-coding RNAs, and three-dimensional genomics. They also discussed the challenges and perspectives along this line for future research in rice.

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A global challenge in crop production in general and rice production in particular is the excess application of fertilizers in an effort for high yield, which not only increases production cost, but also causes severe environmental problems. A consensus for solving this problem is to improve the nutrient use efficiency of the crops. In the review entitled Improvement of nutrient use efficiency (NUE) in rice: current toolbox and future perspectives, Zhang et al. (2020) summarized the progress in molecular dissection of genes for NUE by reverse genetics on macronutrients (N and P) and micronutrients (Fe, Zn, and Se) and also the effort in exploring natural variations for improving NUE in rice. They showcased the current genetic toolbox and offered future perspectives for improving rice NUE.

Studies in rice, Arabidopsis, and other plants have identified a number of CCT domain-containing proteins that play important roles in flowering and yield. CCT family genes are known to be involved in circadian clock and photoperiodic flowering and thus help plants set a suitable flowering time to produce offspring. CCT family genes are also found to be associated with biomass and grain yield as well as photosynthesis, nutrition use efficiency, and stress tolerance. In the paper entitled CCT domain-containing genes in cereal crops: flowering time and beyond, Liu et al. (2020) systematically reviewed the progress in functional characterization of CCT family genes in flowering, geographical adaptation and grain yield formation. The paper also investigated the key questions related to the molecular mechanisms of these proteins and discussed how to use the CCT genes in genetic improvement of cereal crops.

In the entire history of human society, rice has mainly been used as a source of calorie because people usually eat well-milled polished rice grain, while its nutritional value has mostly been neglected. The paper by Zhao et al. (2020), entitled Improving nutritional quality of rice for human health, reviewed the nutritional facts of rice grain including the levels of γ-aminobutyric acid, resistant starch, lysine, iron, zinc, β-carotene, folate, anthocyanin, various carotenoids, and flavonoids. It also investigated the knowledge-base about their synthesis and metabolism and the advances in their biofortification via both conventional and genetic engineering strategies. It was concluded that besides calorie, rice has the potential to become a source of various essential nutrients or bioactive compounds through appropriate genetic improvements to benefit human health.

Large-scale resequencing of the massive rice germplasms has displayed new landscapes of the genetic architecture of the global rice populations and, in combination with phenotyping, also provided gateways to track down the genes for many agronomically important traits. In the paper entitled Advances in genome-wide association studies of complex traits in rice, Wang et al. (2020a) presented an overview of the process in a typical GWAS, including population design,

genotyping, phenotyping, and analysis methods. They also provided recent examples of rice GWAS all the way toward functional characterization of candidate genes. The possible breakthroughs of rice GWAS in the next decade were discussed with regard to the application in breeding, the consideration of epistatic interactions, and in-depth functional annotations of DNA elements and genetic variants throughout the rice genome.

In the last several decades, the conflicts between rice production and environmental resources are becoming increasingly acute. For this reason, scientists in China have proposed the concept of Green Super Rice (GSR) for promoting resource-saving and environment-friendly rice production, while still achieving a yield increase and quality improvement. GSR is becoming one of the major goals for rice research and improvement worldwide, which aims to mine and use vital genes associated with superior agronomic traits such as high yield, good quality, nutrient efficiency, and resistance against insects and stresses. The GSR projects also have aimed to establish genomic breeding platforms and resource-saving and environment-friendly cultivation management systems. GSR has been introduced into eight African and eight Asian countries and has contributed significantly to rice cultivation and food security in these countries. The article entitled Genomic breeding of Green Super Rice varieties and their deployment in Asia and Africa by Yu et al. (2020a) outlined the GSR concept, recent research progress, and the significant achievements in GSR breeding and application.

Maize is a major source of food supply for human and livestock and more recently for biofuels. Maize also has a long history of cultivation in Asia, although it is not native to this continent. The area of maize cultivation has been increasing rapidly in the past two decades in Asian countries especially in China. Five maize papers are included in this issue covering various aspects of maize genetic research, including one original research paper and four reviews.

Over half of the storage proteins in maize kernels are zeins, which are encoded by a large super-gene family. During the development of endosperm, zeins accumulate in protein bodies, which are derived from the rough endoplasmic reticulum. In recent years, great progress has been made in understanding of the zein biosynthesis pathway and its deposition in endosperm. Li and Song (2020) summarized the current understanding of zeins, including the genes encoding these proteins, their expression patterns and transcriptional regulation, the process of protein body formation, and other biological processes affecting zein accumulation.

Drought is the most important abiotic stress to maize production. It is estimated that more than 60% of the maize growing area in China suffers from drought. The genetic basis of maize tolerance to drought stress is very complex. Transcription factors that regulate gene expression are

involved in comprehensive resistance to multiple environmental stresses in maize. Leng and Zhao (2020) summarized the major drought-tolerant transcription factors and their involved regulatory network in maize. It is expected that the discovery and utilization of more drought-tolerant transcription factors will benefit maize tolerance to drought stress.

Epigenetic regulation plays a vital role in the control of complex agronomic traits. Therefore, epigenetic variation contributes to phenotypic diversity and can be used to improve crop quality and productivity. Recent advances in high-throughput sequencing technology make it possible to study the epigenetic landscape on a genome-wide scale. Yu et al. (2020b) summarized recent epigenetic studies in maize, including DNA methylation, post-translational modification of histones, chromatin remodeling, and non-coding RNAs. The findings may have great potential to improve agronomic traits and environmental adaptability of the maize crop.

Hybrid vigor, also known as heterosis, has been widely used in enhancing crop production. However, the molecular mechanisms underlying heterosis are still not fully understood. To provide a more complete understanding of the transcriptomic dynamics associated with heterosis, Luo et al. (2020, published in an earlier issue) generated and analyzed massive sequence data of linear mRNA transcripts and circular RNAs (circRNAs), collected from seedling leaves of two widely used maize inbred lines and their F1 hybrid. They found a significant correlation between linear transcripts and circRNAs resulting from the same locus, suggesting a potential regulatory crosstalk between them. This study demonstrated dynamic variations for linear and circular transcriptomes in the classic hybrid triplet of maize.

It has been suggested that the history of plant breeding could be divided into three major stages, and Breeding 4.0 was proposed to be the next era of plant breeding, which is characterized by the integration of multidisciplinary technologies, including genomics and phenomics, gene editing and synthetic biology, and big data and artificial intelligence. Jiang et al. (2020a) proposed a new maize breeding pipeline, "genomic design breeding", that incorporates doubled haploid production, genomic selection, and genome optimization, and is facilitated by different scales of trait predictions and decision-making models. The successful implementation of the proposed model may promote the evolution of maize breeding from "art" to "science" and eventually to "intelligence" in the Breeding 4.0 era.

Asia is also the largest producer of wheat among all the continents, with China and India as the two major countries. Like rice, wheat also originated and has been cultivated for thousands of years in Asia. During the past decade, two significant advances have been achieved in wheat genetic research. First, genome sequences of common wheat and its relative species have been released.

Second, a highly efficient gene transformation system in wheat is developed by the Japan Tobacco Company and has been widely used in many countries. These developments have greatly speeded up wheat gene mapping and map-based cloning as well as molecular marker development and application in wheat breeding programs. Five articles enclosed in this special issue extensively reviewed the advances of wheat genetic research in various aspects.

Rasheed et al. (2020) summarized 57 homeologous genes underlying important traits and multiple strategies used for their discovery. They discussed the complementary advances in wheat phenomics and analytical approaches to understand the genetics of wheat adaptability, resilience to climate extremes and resistance to pest and diseases. They also indicated that new pan-genome sequencing resources of wheat will strengthen the foundation required for accelerated gene discovery. High-throughput phenotyping and genotyping platforms will provide more opportunities to practice the knowledge-based breeding.

Wang et al. (2020b) reviewed the genomic and functional genomic information obtained in the last 10 years on genes encoding gluten proteins, and the *cis-* and *trans-*factors regulating their expression in wheat grains. They elucidated the involvement of gluten proteins in several wheat sensitivities affecting genetically susceptible human individuals. The new insights gained, together with the availability of precise, versatile, and high-throughput genome editing technologies, promise to speed up the concurrent improvement of wheat end-use and health-related traits and development of high-quality cultivars for different consumption needs.

Ma et al. (2020a) reviewed different aspects of the worldwide most devastating wheat disease, Fusarium head blight (FHB). These include FHB incidence, epidemics and impact, causal *Fusarium* species, distribution and virulence, types of host resistance to FHB, germplasm exploitation for FHB resistance, genetic control of FHB resistance, fine-mapping of resistance genes such as *Fhb1*, *Fhb2*, *Fhb4,* and *Fhb5*, and also molecular cloning of *Fhb1*, omics-based gene discovery and resistance mechanism study, and breeding for better FHB resistance. It was pointed out that although the advances made in this area are outstanding and exciting, it is still a long way to overcome FHB due to the complicated nature of resistance to hemi-biotrophic pathogens like *Fusarium* species and lack of immune germplasm.

Gupta (2020) summarized the available information on wheat genetics of some important quantitative traits including yield and its components, tolerance to abiotic stresses (heat, drought, salinity and pre-harvest sprouting), and biofortification (Fe/Zn and phytate contents). Major emphasis was laid on recent literature on QTL interval mapping and genome-wide association studies, giving lists of known QTL and known marker–trait associations for the traits of interest.

For each trait, an account of the present status of marker-assisted selection was included.

Wang et al. (2020c) reviewed the advances in genetic transformation of wheat. This development enabled significant progress in wheat genome editing technologies including zinc finger nucleases (ZFN), transcription activator-like effector nuclease (TALEN), and cluster regularly interspaced short palindromic repeats (CRISPR) associated endonucleases (Cas). Among these, the CRISPR-Cas9 is highly specific and most efficient and has been widely used in genetic engineering. These technologies will help biologists and biotechnologists better understand the processes of mutagenesis and genomic alteration and play an important role in improvement of wheat varieties.

Yellow mosaic virus is the pathogen causing serious disease in many plants; leaf rust diseases cause significant yield losses in cereals. This special issue invited two papers addressing these two diseases in wheat and barley.

The *Bymovirus*-induced yellow mosaic diseases seriously threaten global production of autumn-sown barley and wheat. Jiang et al. (2020b) presented a global overview on *Bymovirus* resistance in these cereal crops. *Barley yellow mosaic virus* and *Wheat yellow mosaic virus* of the family *Potyviridae* are transmitted by soil-borne plasmodiophorid *Polymyxagraminis*. Host specificity of these viruses, as well as the genetically identified resistance genes in barley, wheat, and wild relatives, were documented. Moreover, germplasms and large-scale sequencing, the exploration and isolation of corresponding resistance genes were comprehensively reviewed. The prospected advances on cloning of the resistance or susceptibility genes and the benefits for marker-assisted resistance breeding were discussed.

The leaf rust diseases of cereals cause significant yield losses, posing challenges to global food security. The deployment of resistance genes has long been considered as the most effective and sustainable way to control cereal leaf rust diseases. Dinh et al. (2020) reviewed recent studies on the defense mechanisms conferred by the leaf rust resistance genes identified to date in cereals and their roles in either pattern-triggered immunity (PTI) or effector-triggered immunity (ETI). They highlighted latest strategies based on advances in genome sequencing and gene isolation by overcoming the complexity of cereal genomes. The leaf rust resistance genes cloned so far from wheat and barley belong to various protein families, including nucleotide-binding site/leucine-rich repeat (NLR) receptors and transporters.

Common buckwheat is an annual crop domesticated in Asia and is now cultivated widely around the world. The grain contains abundant nutrients and bioactive compounds, and much research has been done to improve the yield and eliminate the proteins that cause allergic reactions in some people. Matsui and Yasui (2020) summarized recent developments of buckwheat breeding materials, tools, and methods, including the development of self-compatible lines, genetic maps, and genome database. They also presented strategy for efficient breeding and emerging breeding methods for high-value lines.

Food legumes are a major crop group in Asia as they have unique features including their role in human and animal nutrition, nitrogen fixation, adaptation to stress conditions, suitability to various cropping systems, and for overall sustainability of agricultural production systems. While the majority of cereal crops in Asia have attained self-sufficiency, the availability of legumes is still low. As a result, many Asian countries are importing legumes costing huge amounts of foreign exchange. Furthermore, dependence on only a few legumes in production and market chain and high demand lead to increased prices for legumes. Consequently, the poor rural and urban families cannot afford to eat legumes to the desired level to meet protein needs. One of the key reasons for low crop productivity is the limited use of genetic diversity and modern breeding methods in crop improvement programs in Asia. With an objective to accelerate genetic gain, this special issue included articles on four key legume crops namely soybean, groundnut, chickpea, and pigeonpea. While led by researchers mainly from China and India, these articles have international flavor and provide an up-to-date status on research in these crops at the international level with special emphasis in Asia. All these articles also provide a way forward for crop genetics research and molecular breeding for developing better varieties in Asia.

In the case of soybean, Li et al. (2020) presented the current status of soybean genomics research including reference genomes, re-sequencing efforts, and molecular mapping in three key countries in Asia, namely China, South Korea, and Japan. Authors also highlighted the key examples of molecular breeding for resistances to some biotic and abiotic stresses including the soybean cyst nematode in Asian countries. It was anticipated by authors that genome-wide association analysis, genomic selection, and genome editing would become essential tools for assessing favorable alleles in the germplasm and combining them to develop new cultivars.

Groundnut is an important crop in several Asian countries. However, China and India contribute to 42% and 18% global groundnut production, respectively. Pandey et al. (2020) presented a critical appraisal on groundnut genomics research and its translation for groundnut improvement at the international level. They discussed progress on several key milestones in genomics research including genome sequence assemblies, resequencing of diverse germplasm lines, genome-wide transcriptome atlas, and cost-effective high- and low-density genotyping assays. Authors presented the utility of these genomic resources to perform high-resolution trait mapping and development of diagnostic markers. Some success stories on development of molecular breeding

products were also documented. The authors anticipated the use of genomic selection, speed breeding, and genome editing approaches in coming years.

Chickpea and pigeonpea are important pulse crops in India, which is the largest producer and importer of these crops. For chickpea, Roorkiwal et al. (2020) updated on recent advances in genomic tools and technologies including genome assemblies, re-sequencing efforts, pan-genomics, genotyping platforms, etc. The authors provided a report on QTL mapping of important traits, omics technologies, and GWAS analysis as well as successful molecular breeding stories. They envisioned to use a sequence-based holistic breeding approach, including the integration of functional omics, parental selection, forward breeding, and genome-wide selection in future chickpea improvement programs.

In the case of pigeonpea, Bohra et al. (2020) presented a report on genomics research and genomics-assisted breeding efforts for pigeonpea improvement. The authors outlined the developments of genomic resources such as genome-wide markers, high-throughput genotyping assays, saturated genome maps, marker/gene–trait associations, whole-genome sequence, and germplasm resequencing data. It was suggested to embrace new breeding tools like genomic selection and speed breeding for enhancing precision and efficiency in both hybrid breeding and varietal improvement.

Vegetable crops are major nutrient sources for humanity and have been widely cultivated for thousands of years in all the Asian countries. Rapid progress has also been made in genomic research in a number of vegetable crops, which has enhanced the understanding of biology of vegetable plants and enabled the developments of new breeding technologies. Four papers were included in this special issue as a glimpse of genetic research in vegetable crops.

Hao et al. (2020) outlined the present genome-based breeding approaches used for major vegetable crops to provide a view of next-generation molecular breeding. The important agronomic traits of vegetable crops, such as disease resistance, fruit flavor, fruit shape, and plant architecture, are main targets for modern breeding. The reference genome of more than 20 vegetables has been well assembled and published, and the advance of sequencing and molecular technologies has enabled the recognition of the genomic structure of these vegetables. The availability of a nearly unlimited number of markers has accelerated the speed of QTL identification and gene cloning. Genome-based breeding has been utilized in many vegetable crops, including Solanaceae, Cucurbitaceae, Cruciferae, and other families, thereby enabling selection at a single-nucleotide level. High-throughput genotyping has become one of the most popular methods in vegetable breeding. Gene-editing technology may greatly improve breeding efficiency of vegetable crops, especially in combination with various omics technologies and information.

Tomato is one of the major cultivated vegetables worldwide and has emerged as the model system for the investigation of fleshy fruit. Ma et al. (2020b) systematically summarized recent advances in the regulation of tomato fruit ripening by non-coding RNAs (miRNAs, siRNAs, lncRNAs, and circRNAs). These RNAs are involved in a number of processes including ethylene biosynthesis and signal transduction, pigment accumulation, flavor and aroma compound formation, fruit softening, and their coordinated regulation on tomato fruit ripening, which provides a foundation for understanding the molecular biology of fleshy fruit ripening.

Sun et al. (2020) updated the reader on the main advances of complex trait dissection in tomato by omics since the release of the tomato genome sequence in 2012. They summarized the genes identified which control complex traits of this crop. These findings provided insight into the regulation of some tomato complex traits as gained by the characterization of the causal genetic variants. The paper also explored the utilization of CRISPR/Cas9 for the modification of tomato complex traits.

Cucumber (*Cucumis sativus* L.) is an important vegetable cultivated in Asia and also many countries worldwide. With increasing consumption demand, the production of Cucurbitaceae crops has been increasing rapidly. Thus, new cultivars that can produce high-quality cucumber with high yield and easy cultivation are in need. The paper by Feng et al. (2020) summarized the achievements of conventional cucumber breeding such as crossing and mutagenesis. The review focused on the current status of molecular breeding of cucumber in China, including the progress in cucumber genomics and characterization of molecular mechanism underlying important agronomic traits. Large efforts were also made in the creation of high-quality multi-resistant germplasm resources, new variety breeding, and ecological breeding. Future development trends and prospects of cucumber molecular breeding in China were also discussed.

In addition to discussing genetics research and molecular breeding in different crops as mentioned above, Jaganathan et al. (2020) compared different marker systems used for fine mapping and QTL cloning in the pre- and post-next-generation sequencing era. They opined that efficient genotyping/sequencing assays may circumvent the need for cumbersome procedures that were earlier used for fine mapping and gene cloning. As a result, it will help to enhance understanding of the trait architectures of agricultural significance to accelerate crop improvement.

Finally, we should note that because of space limitation and the wide diversity of the crops in Asia, this special issue only presents a very modest sample for the vast scale of crop genetics research in Asia. We were not able to select as many topics as we wished to cover as many crops in the Asian crop science community as they deserve in such a special issue. We thank the Editor-in-Chief, Professor Albrecht

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