Maize genetics, genomics, and sustainable improvement

David Jackson · Feng Tian · Zuxin Zhang

Accepted: 8 November 2021 / Published online: 27 December 2021
© The Author(s), under exclusive licence to Springer Nature B.V. 2021

Maize, or corn, is the most highly produced crop worldwide, with a global production output of more than 1.1 billion tons in 2020 (<https://www.statista.com/statistics/263977/world-grain-production-by-type>). This is almost double the global production of rice, and more than wheat, barley, and other grains combined. This high level of production provides grain for diverse purposes, not only food, but also animal feed, biofuels, and industrial raw materials. While the USA is a major producer, maize is truly a global crop, with significant production in China, Europe, South America, and other areas. In the USA, where large-scale corn production started, yield has

increased around six-fold since the 1930s (<https://www.worldofcorn.com>). This has been achieved through a number of innovations, particularly the application of heterosis or hybrid vigor, breeding for increased yield, and improved agronomic practices. Despite these major advances, there is an urgent need to maintain productivity in the face of climate change, and also to improve the sustainability of agriculture by improving yield while reducing energy intensive inputs. This special issue, proposed by Editor-in-Chief of *Molecular Breeding*, Prof. Qifa Zhang, focuses on maize genetics, genomics, and sustainable improvement. Eleven papers are published in this issue, and review and provide future insights into maize developmental biology, the genetic basis of yield-traits, the genetic basis of abiotic and biotic stress tolerance, and breeding technology. Here, we summarize some highlights from these papers.

This article is part of the Topical Collection on *Maize Genetics, Genomics and Sustainable Improvement*

D. Jackson
Cold Spring Harbor Laboratory, Cold Spring Harbor,
NY 11724, USA
e-mail: jacksond@cshl.edu

D. Jackson · Z. Zhang (✉)
National Key Laboratory of Crop Genetic Improvement,
Huazhong Agricultural University, Wuhan 430070, China
e-mail: zuxinzhang@mail.hzau.edu.cn

F. Tian (✉)
State Key Laboratory of Plant Physiology
and Biochemistry, National Maize Improvement Center
of China, and Center for Crop Functional Genomics
and Molecular Breeding, China Agricultural University,
Beijing 100193, China
e-mail: ft55@cau.edu.cn

Maize developmental biology

The wild ancestor of maize, teosinte, grows to this day in Mexico where it was domesticated starting around 10,000 years ago. Domestication led to major remodeling of plant architecture, turning the bushy, weedy teosinte plant into compact modern corn that usually makes only a single stalk, with large ears and kernels. A major contributor to increasing yield has been higher planting density, facilitated by plants with more upright leaves. The review by Josh Strable

(2021) describes how plant architecture was remodeled during domestication, and gives insights into some of the genes that have been selected to enable maize to become such an important crop. The review features beautiful pictures and illustrations, describing leaf, meristem, and whole plant anatomy, and describes that natural variation in these features can be exploited in breeding programs. Perspectives are discussed for using knowledge of maize development in the context of integration of alleles from teosinte, and use of pan-genomes and genome editing to further enhance productivity. Perhaps the most dramatic transformation from teosinte to maize was the conversion of their tiny ears into the huge ears of modern maize. A beautifully illustrated review by Chen and Gallavotti (2021) describes how maize inflorescences develop, including important insights into how developmental genes interact with environmental factors, important when considering how maize will perform under a changing climate. Another dramatic change in domestication was the large increase in kernel size. A comprehensive review of kernel development by Dai et al. (2021) provides insights into the many genes involved, as well as synthesizing knowledge about the functions into a model of how they interact. Better knowledge of these genes will no doubt foster applications in improving maize productivity.

Genetic basis of yield-traits

Genetics is a major tool used by breeders to enhance yield. An article by Zhang et al. (2021) performs a meta-analysis of yield-related trait QTLs to identify 49 consensus cQTLs, followed by association mapping to identify some of the underlying genes. These are nicely summarized in a genome-wide view and a schematic of the different pathways involved, and how they can be applied in breeding. The power of combining different approaches in discovering molecular mechanisms underlying yield, and how this knowledge can be applied in future breeding is also discussed. Breeding is historically a slow process that has been significantly improved using genomic selection methods. A review by Rice and Lipka (2021) describes how genomic selection models could be improved to speed up this process even more. The article provides an insightful review of the history of maize breeding, and explains the use of genomic

selection and how it can be improved by incorporating environmental and omics data. Future prospects using simulation software and machine learning are also discussed.

Genetic basis of abiotic and biotic stress tolerance

Crop yields are strongly affected by both biotic and abiotic stresses, which are predicted to become more prevalent with the advent of climate change. Therefore, breeding for yield in different environments, and yield stability, is an important goal. A review by Zhu et al. (2021) describes the state of progress in understanding the genetic basis of maize diseases, which reduce yields by up to 14%. A comprehensive summary of different diseases is presented, along with images of their effects on plant growth. Efforts to alleviate the impact of diseases using knowledge of naturally occurring resistance genes in traditional breeding, genomic selection, or transgenesis are described. Future insights include the need to identify more quantitative disease resistance genes, as well as to understand how they function and how they can be incorporated using genome editing. Maize is predominantly rain fed, so is also prone to drought, especially at flowering and seed set. A review by Liu and Qin (2021) provides an excellent overview of quantitative genetic and omics approaches that have been used to study drought stress in maize. Details of some of the drought associated loci that have been identified and their contribution to breeding drought resistance are presented. The application of multi-omics approaches to further understand mechanisms of drought stress, and how they might be applied is also discussed. On the opposite end of the water spectrum, waterlogging is also a serious problem for maize growth, and will only get worse as our climate becomes less predictable. A review by Liang et al. (2020) described the effects of waterlogging on maize growth, some of the mechanisms involved, and efforts to improve maize responses to this abiotic stress. QTL experiments have identified some of the genes involved, and an outline of a possible genetic network is presented. Attempts to alleviate this stress using breeding or transgenic approaches are described; however, relatively little is known in maize compared to other plant

species, so knowledge from those systems could help advance maize research in this area.

Maize breeding technology

Generation of inbred lines used to make productive hybrids is a cornerstone of maize breeding. Methods to make inbreds were revolutionized by the discovery of lines that produce spontaneous haploids that can be doubled to make perfect inbred diploids. A review by Meng et al. (2021) describes different ways in which haploids can be produced, including recent updates on the molecular mechanisms involved. It also describes how haploids can be detected, and how they can be doubled, as well as various uses, for example, in gene editing in diverse lines, and a potential use to develop apomixis. Despite its almost universal use, ways in which haploid technology could be improved are described. A more recent innovation in maize breeding is the application of CRISPR-Cas systems for genome editing. A comprehensive review by Nuccio et al. (2021) describes the history of genome editing, and a guide to how the different CRISPR systems work. It also describes many uses of this technology in basic research and in product development, and outlines ways in which the technology could be improved. The application of CRISPR, as well as many other potential technologies to improve maize productivity, relies on plant transformation and regeneration. A very detailed review by Kausch et al. (2021) describes the history of maize transformation technology, and approaches that are greatly improving its efficiency, including the use of developmental genes to promote regeneration. These advances will bring multiple benefits, including more easy production of transgene-free gene-edited lines, and more precise genome arrangements to better engineer maize traits. This review, like many in the special issue, contains spectacular illustrations that will be great for teaching.

Overall, this maize special issue provides comprehensive and exciting updates into the innovative approaches that are being used to improve our understanding of maize as a species, and improve its sustainable use in agriculture.

Author contribution David Jackson, Feng Tian, and Zuxin Zhang were responsible for inviting and handling all the papers. David Jackson wrote the editorial and Feng Tian and Zuxin Zhang edited it. **References**

- Chen Z, Gallavotti A (2021) Improving architectural traits of maize inflorescences. *Mol Breeding* 41:21
- Dai D, Ma Z, Song R (2021) Maize kernel development. *Mol Breeding* 41:2
- Kausch AP, Wang K, Kaeppler HF, Gordon-Kamm W (2021) Maize transformation: history, progress, and perspectives. *Mol Breeding* 41:38
- Liang K, Tang K, Fang T, Qiu F (2020) Waterlogging tolerance in maize: genetic and molecular basis. *Mol Breeding* 40:111
- Liu S, Qin F (2021) Genetic dissection of maize drought tolerance for trait improvement. *Mol Breeding* 41:8
- Meng D, Liu C, Chen S, Jin W (2021) Haploid induction and its application in maize breeding. *Mol Breeding* 41:20
- Nuccio ML, Claeys H, Heyndrickx KS (2021) CRISPR-Cas technology in corn: a new key to unlock genetic knowledge and create novel products. *Mol Breeding* 41:11
- Rice BR, Lipka AE (2021) Diversifying maize genomic selection models. *Mol Breeding* 41:33
- Strable J (2021) Developmental genetics of maize vegetative shoot architecture. *Mol Breeding* 41:19
- Zhang H, Lu Y, Ma Y, Fu J, Wang J (2021) Genetic and molecular control of grain yield in maize. *Mol Breeding* 41:18
- Zhu M, Tong L, Xu M, Zhong T (2021) Genetic dissection of maize disease resistance and its applications in molecular breeding. *Mol Breeding* 41:32

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.