Maize biology: From functional genomics to breeding application[™]

Editorial

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Maize (*Zea mays* L.) is one of the most important crops globally for food, feed, and fuel. Maize grain production has increased more than eight-fold in the past century to a current annual global production of one billion tons (http://faostat.fao.org/). By 2050, it will require 70% more food than today's consummation since the population size will increase to 9 billions. It is estimated that maize will contribute more than half of the increased demand for cereals in the future. Thus, there is a tremendous innovation stream for maize breeders to utilize in their attempts to substantially increase maize productivity in an environmentally sensitive way (FAO 2009).

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In the course of life science research for more than a century, maize has been used as a model system in basic research in cytology, genetics, genomics and others. This is not only because of its botanical characteristics of monoecious and heterologous flowers, which is easy to construct in various genetic segregation populations, but also because of its biological characteristics of cross-pollination, resulting in abundant genetic diversity (Yan et al. 2011). There is one single nucleotide polymorphism per 44bp in its genome, and the diversity between any two maize lines is even greater than that between human beings and chimpanzees (Gore et al. 2009). This huge genetic diversity provides infinite space for maize genetic improvement.

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With the further decrease of sequencing price, especially the vigorous development of third generation sequencing technology, new opportunities have been brought for maize functional genomics research. Since the publication of maize B73 reference genome in 2009 (Schnalbe et al. 2009), three new maize reference genomes were assembled and released by 2018 and 2019 (Springer et al. 2018; Sun et al. 2018; Yang et al. 2019). Now, Maize GDB contains 12 complete maize genomes and is expected to increase to 40 by 2020. MaizeGDB has also developed a variety of tools to improve the retrieval, display and utilization of data (Portwood et al.

2019). The progress of genome research has greatly promoted the research of maize functional genomics, and a large number of functional genes affecting various traits including agronomic, yield, quality, biotic and abiotic traits and so on have been cloned and applied for breeding (Xiao et al. 2017).

Among the main food crops, maize is also a relatively balanced crop with relatively high starch and protein, but also rich in carotenoids, tocopherols, folic acid and other micronutrients (Wen et al. 2016). Micronutrient deficiency, known as "hidden hunger", has been a global challenge to improve the content of micronutrients in stable food crops such as maize through biofortification and is therefore an economically and socially sound way to address this challenge. In this Special Issue, we collected seven articles to show the latest research progress in maize functional genomics in China from different perspectives.

A genome-wide association study strategy was used to identify the genes associated with salt stress (Luo et al. 2019). A total of 57 genetic variants (loci) were detected to be significantly associated with the salt-tolerant phenotypes, and 49 candidate genes were identified among these loci. The function of two candidate genes was validated in Arabidopsis. The results of this study deepen our knowledge of maize salt tolerance. The genes have the potential to be used as molecular markers in breeding of salt-tolerant maize cultivars in the future. Guo et al. (2019) used the quantitative trait loci (QTL) mapping strategy to explore the genes associate with folate content in mature kernels. Two major folate QTL on chromosome 5 were mapped which contributed 41.6% of the phenotypic variation of 5-formyltetrahydrofolate, the most abundant storage form among folate derivatives, which is of great importance for human health. Their fine mapping and functional analysis will reveal details of folate metabolism, and provide a basis for marker-assisted breeding aimed at the enrichment of folates.

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Qin et al. (2019) identified two transporters *ZmHAK*5 and *ZmHAK*1 which play crucial roles in K⁺ homeostasis and cell growth. *ZmHAK*5 acts as a high-affinity K⁺ transporter that mediates K⁺ uptake in roots under K⁺-limited conditions, while *ZmHAK*1 may regulate K⁺ distribution in shoots. Genetic manipulation of ZmHAK5 may represent a feasible way to improve K⁺ utilization efficiency (Qin et al. 2019).

Two kernel mutant genes were identified and verified (Song et al. 2019; Zuo et al. 2019). OS1 (opaque endosperm and small germ 1), encoding a putative RWP-RK transcription factor, expresses highly in the nutrient-allocation cell types of maize endosperm (Song et al. 2019). Transcriptome analysis revealed that a lot of genes in specific cell types are down-regulated in the os1 mutant, including ZmMRP-1 and Meg1 in basal endosperm transfer layer cells and a majority of zein- and starch-related genes in central starch endosperm cells. Mutation of OS1 results in unbalanced nutrient allocation between endosperm and embryo in maize kernels. A similar finding was also recently reported for the same gene (Mimura et al. 2018). Dek42 is a new gene, encoding an RRM RBM48 type RNA binding protein, and mainly functions in intron-alternative splicing particularly for the U12-type introns (Zuo et al. 2019). The study provides evidence that DEK42 regulates alternative intron splicing via interacting with the spliceosome components SF3a1 and U1-70K. The same gene was also recently reported by another group from the University of Florida (Bai et al. 2019).

The SWI/SNF (SWItch/Sucrose Non-Fermentable) chromatin remodeling factor deficient in DNA methylation 1 (DDM1) has been demonstrated to play key roles in mediating all three contexts of DNA methylation in parallel with the RNA-directed DNA methylation (RdDM) pathway in *Arabidopsis* (Zemach et al. 2013). However, in maize, DDM1 is newly identified to regulate the formation of mCHH islands via the RdDM pathway, highlighting that the machineries of DNA methylation are evolutionarily diverged in different species (Long et al. 2019). This mechanism was also revealed in another independent study (Fu et al. 2018).

Short-term straw returning and tillage practices significantly altered the diversity, relative abundance and functions of the soil microbiome. Rotary tillage and straw returning (RTS) combination possessed the highest bacterial diversity and lowest ratio of G^+/G^- bacteria, indicating that RTS could be an efficient integrated management system to improve the microbiome in the short term. *Mycobacterium* and *Methylibium* could serve as biomarkers for RTS (Xia et al. 2019).

The Special Issue covers a wide range of topics. However, it still only covers very few directions in maize biology. At present, the maize functional genomics research in China is flourishing, and new technologies and fields are endlessly emerging. More knowledge gained from basic research has been applied to breeding to make due contribution to ensuring food security. At the same time, we also note that the competition and repetition of functional genomics research are also increasing. Three of the seven articles in this issue overlapped with work in other research groups in the world. How to further strengthen international collaboration and communication to reduce redundant work and increase efficiency has become an urgent issue for the maize community. As the importance of maize research calls, we need more young talents to join the maize research community. At the same time, we need to cooperate and win-win.

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