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Editorial

Genes, Genetics and Breeding of Tomato

Pingfei Ge [1] and Yuyang Zhang [1,2,3,4,*]

1 National Key Laboratory for Germplasm Innovation and Utilization of Horticultural Crops, Huazhong Agricultural University, Wuhan 430070, China; gepingfei1997@163.com
2 Hubei Hongshan Laboratory, Wuhan 430070, China
3 Shenzhen Institute of Nutrition and Health, Huazhong Agricultural University, Wuhan 430070, China
4 Shenzhen Branch, Guangdong Laboratory for Lingnan Modern Agriculture, Genome Analysis Laboratory of the Ministry of Agriculture, Agricultural Genomics Institute at Shenzhen, Chinese Academy of Agricultural Sciences, Shenzhen 518000, China
* Correspondence: yyzhang@mail.hzau.edu.cn; Tel.: +86-27-87282010

1. The Increasing Importance of Genes and Genetics in Tomato Breeding

Tomato (*Solanum lycopersicum*) is widely cultivated and is one of the most important vegetable crops in the world, with great economic significance. During the past two decades, tomato production has increased two-fold, which is largely the result of genetic improvement toward high yield and adaptation. Over the years, the goals of the genetic breeding of tomatoes have targeted productivity and tolerance to pests and diseases. Consumers demand high nutritional and taste quality, and producers demand tomato fruit that is easy to cultivate with high adaptation to stress or disease. Fortunately, tomato is a vegetable crop that is rich in genetic resources and could serve as a model for fruit biology and plant genetics. Great progress has been made in understanding the genes and genetics underlying its important traits, e.g., fruit development, yield, quality, abiotic stress adaptation and disease resistance. These genes facilitate tomato improvement based on molecular approaches. Indeed, molecular breeding technology has been widely applied in tomato improvement. The advances in tomato genetics and genomics have paved the way for tomato molecular breeding. Improving the yield, quality and stress tolerance of tomato is the common goal of breeders, producers and consumers. For this reason, this Special Issue on "Genes, Genetics and Breeding of Tomato" will present the advances in gene mining, genetic mechanism and molecular breeding of tomato.

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2. Application of Omics in the Study of Tomato Biotic Stress

As one of the most widely planted vegetable crops in the world, tomato is very vulnerable to various pests and diseases during its growth. Transcriptomics and metabolomics have been applied widely in the study of stress response. The analysis of differentially expressed genes and accumulated metabolites may reveal new mechanisms of plant stress response.

Bacterial canker of tomato is caused by *Clavibacter michiganensis* (*CM*), which can even cause 100% yield loss in severe cases. There are two possible sources of disease resistance in wild tomato plants: one affects the growth of *CM* by releasing specific substances in xylem sap, and the other is the lack of some in vivo signals that activate the virulence of *CM* [1]. A susceptibility gene, *WAKL20*, was screened out via transcriptome profiling of the resistant inbred line IBL2353 and susceptible line Ohio88119. The inactivation of the *WAKL20* gene led to more durable and broad-spectrum resistance [2]. By comparing genes differentially expressed in plant–pathogen interactions, *WRKY41* and *CBEF* were identified as genes highly expressed upon infection, indicating that they may be involved in the defense against *Fusarium* spp. [3].

Except bacterial canker, losses caused by the yellow leaf curl virus cannot be ignored. As a new disease-resistant gene, *TY5* has gradually attracted attention from breeders, but the accuracy of its marker detection has hindered the development of tomato breeding to a certain extent. High-resolution melting (HRM) is based on the markers developed within a gene but is not affected by segregation and recombination, thus completely overcoming the false-positive problem of linkage markers. The HRM marker of *TY5* showed a high accuracy of 100%, consistent with the phenotype, and will greatly improve the efficiency of breeding [4].

Insect damage is also one of the factors restricting tomato production. Recent studies have shown that zingiberene (ZGB) produced by plants plays an important role in pest control [5]. Panizzon Diniz et al. proved the relationship between ZGB and insect resistance by measuring the ZGB content in BC_3F_2 and parent populations. The number of whitefly eggs and nymphs that survived in plants with low ZGB was eight and six times higher than that in tomato plants with high ZGB. The effective biological control of *Tuta absoluta* using ZGB was also confirmed. These data showed that the content of ZGB can confer insect resistance in plants and can provide an alternative approach for crop resistance breeding.

3. Genes Underlying Tomato Response to Abiotic Stress

In addition to biotic stress, abiotic stress is another major factor affecting tomato production. Abiotic stress is mainly a challenge in the survival of plants brought about by environmental factors such as temperature and water.

RanBP2-type zinc finger proteins are involved in the regulation of mRNA processing in animals, but their functions in plants remain unclear. Gao et al. identified a total of 22 family genes in tomato using bioinformatics approaches. Further research showed that most of the genes responded to at least one of four stress treatments (cold, heat, drought and salt), indicating that this family may have a corresponding function in abiotic stress responses [6].

Chilling damage brings about great challenges to the autumn production of tomatoes. Numerous studies have reported the effect of low temperature on tomato fruit, but few have been reported on the effect of N^6-methyladenosine methylation on chilling injury. An analysis of the differentially expressed genes in methylated transcripts before and after chilling treatment showed that the methylation levels of genes related to plant hormones and fruit texture were changed. Specifically, the expression of *ACO* increased by four folds, and the expression level of *cpHSC70* decreased by more than 90%, which provides insight into the mechanism of chilling injury to tomato fruits [7].

Drought and other extreme weather conditions brought about by the deterioration of the global environment are increasing. Recent studies showed that in *SlPYL4*-silenced tomato plants, a 6 h drought treatment led to a decease in the activities of SOD, POD and CAT by 20%, 10% and 50%, respectively, compared with the control, indicating a decrease in the ability to drought response. In addition, the expression levels of *SlPP2C1*, *SlPP2C2*, *SlSnRK2.2*, *SlABF4*, and *SlAREB* were significantly increased, while the expression level of *SlSnRK2.1* significantly decreased in *SlPYL4*-silenced plants, which indicated that *SlPYL4* is involved the ABA-pathway-mediated drought response [8].

The exhaust gas produced by industrial production is also deleterious to the growth of plants. Previous studies found that hybrid-proline-rich protein 1 (HyPRP1) is involved in abiotic stress and SO_2 metabolism in tomato. Further studies showed that when SO_2 toxicity occurred, *HyPRP1*-RNAi lines accumulated less hydrogen peroxide and had a higher chlorophyll content relative to WT as well as *HyPRP1*-overexpressing lines, resulting in minimal leaf damage [9].

4. Genes Regulating Tomato Fruit Development and Ripening

Phytohormones play an important role in plant growth, development and environmental response. The brassinosteroid (BR) signaling mutant *Brassinosteroid Insensitive 1* (*bri1*) exhibits a dwarf phenotype, with decreased fruit size and weight [10]. Further studies showed that this phenotype change was due to reductions in cell size and number, and the expression level of *SlSUT1* in the mutant was significantly reduced in the mutant, resulting in a limited energy supply.

The mechanism of ethylene in fruit ripening has been elucidated. Anas et al. introduced the mutant allele *Sletr1-2* into tropical tomato varieties through hybridization and significantly extended the shelf life of tomato fruits [11]. Crosstalk between ethylene and JA occurs to regulate fruit ripening. ERF4, as the core JA signaling central protein JASMONATE ZIM-DOMAIN (JAZ) and the interactor of the ethylene signaling pathway, regulates the ethylene signaling pathway by influencing the binding of the JAZ-ERF4-MYC2 complex with promoters of *ACS1* and *ACO1*, further regulating fruit ripening [12].

5. Toward Tastier Tomato Fruit

Sugar content is an important factor determining the taste of tomato fruit, and sugar transporters play a very important role in the formation of fruit quality. A recent study showed that *SlSWEET12c* regulates sugar accumulation in tomato fruits [13]. The contents of fructose and sucrose increased by 20% and 40%, respectively, in fruits of transgenic tomato overexpressing *SlSWEET12c* while decreased in *SlSWEET12c*-silenced lines.

Grafting, as a way to enhance plant resistance to drought, salinity and soil born disease and to increase yield, has been widely used in horticultural crop production, but there are few studies on the effect of grafting on fruit quality. Rootstock could be used in grafting to modulate the content of glucose, fructose, malic acid, citric acid and volatiles in tomato fruits, while the different combinations of rootstock and scion exerted different effects on fruit quality [14]. In addition to grafting, plant architecture management could also affect fruit quality to some extent. However, the genes and genetics could severe as primary approaches for fruit quality improvement [15].

In the process of the domestication of and improvement in horticultural crops, due to pursuits of increasing yield, cultivated species have lost many stress- or quality-related genes [16]. In recent years, the cooperation between scientists and breeders has been deepening in the era of genomics-based breeding, and it is expected to improve the quality of the fruit while maintaining the original resistance of the plant, which will make human diets healthier.

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