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Editorial

Focus on fruit crops

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Fruit crops are traditionally defined as woody or herbaceous perennials that produce edible fruits. Fruits are major sources of nutrients for humans, and fruit growing is a significant driver for economic growth and development in rural areas and their communities worldwide. The fruit industry faces enormous challenges posed by dramatic changes in global climate, water shortage, and deterioration of the environment. Mechanistic studies in fruit crops have been difficult because of their long juvenility and perenniality. However, recent advances in plant physiology have shed new light on various aspects of fruit crop biology, such as growth, development, ripening, fruit quality, and stress tolerance. One significant advancement in fruit crop physiology is the identification of key genes and regulatory networks that control fruit development and ripening. Another is the investigation of how abiotic stresses, such as drought and low-/high-temperature stress, affect plant growth, yield, and fruit quality. Advances in postharvest technologies have also been significant, allowing for better preservation of freshness and flavor. Nevertheless, there remain challenges and opportunities ahead. Many fruit crops are vulnerable to pests and diseases, which can result in significant losses. Furthermore, climate change poses an increasingly serious threat to fruit production as it alters weather patterns and exacerbates environmental stress. Addressing these issues requires interdisciplinary collaborations between plant physiologists, geneticists, breeders, and horticulturists.

In this Focus Issue on Fruit Crops, we present a collection of research articles and update reviews that cover the latest research on fruit crops and highlight the current trends and future directions. These advancements not only help us better understand the molecular mechanisms underlying growth and development of fruit crops and their responses to environmental stresses but may also offer strategies for the fruit industry to adapt to consumer demands and the changing environments. Here, we highlight some of the contents of the 8 Updates, 23 Research Articles, and Topical Review presented in this Focus Issue, as well as some in our related Focus Collection.

Abiotic and biotic stresses

In many fruit-growing regions in the world, crop production is drastically affected by environmental stresses, both abiotic and biotic. As climate change further exacerbates these stresses, understanding the mechanisms by which plants cope with these abiotic and biotic stresses is critical for developing resilient crop varieties. In this Focus Issue, Ren et al. (2023) summarize recent major advances in physiological and molecular analyses of cold tolerance in grapevine (*Vinifera* spp.) and strategies for improving its tolerance to cold stress, while Liu et al. (2023b) provide an overview of the effects of drought stress on plant growth and development of fruit crops, and the common pathway regulating drought tolerance in these crops.

Development of crop varieties resistant and/or adaptive to stresses is critical. The future mission of crop improvement should, therefore, emphasize the development of crop varieties with optimal genome plasticity for resistance or tolerance to multiple biotic and abiotic stresses, while improving fruit yield and quality. A conservative estimate

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of the world population by 2050 is around 9.3 billion, which will necessitate an increase of crop production by about 70%.

Understanding how fruit crops respond to stresses and developing stresses-tolerant varieties are critical for sustainable fruit production. MicroRNAs (miRNAs) play an important role in abiotic stress responses in plants. However, the functions of miRNAs and their targets under drought in apple (*Malus domestica*), 1 of the most widely cultivated fruit trees, are unknown. Feng et al. (2023) reported that, in response to drought, microRNA156ab is involved in auxin metabolism by targeting MsSPL13, which regulates the expression of the auxin-related genes *MsYUCCA5*, *MsPIN7*, and *MsGH3-5*. Shen et al. (2023) showed that a double-stranded RNA-binding protein, HYL1, positively modulates transcripts of *MdMYB88* and *MdMYB124*, and the biogenesis of several miRNAs, including Mdm-miR156, Mdm-miR172, and Mdm-miR160, conferring cold tolerance in apple. It is well known that the inducer of CBF expression 1 (ICE1) plays a positive role in plant cold tolerance by promoting the expression of CRT-binding factor (CBF) and cold-responsive (COR) genes. However, how ICE1-interacting transcription factors regulate *CBF* expression and ICE1 function remains unknown. Yang et al. (2023) showed that MdbHLH4 binds to the promoters of *MdCBF1* and *MdCBF3* and suppresses their expression. Furthermore, MdbHLH4 also interacts with MdICE1L, a homolog of AtICE1 in apple, inhibiting the binding of MdICE1L to the promoters of *MdCBF1/3* and thus their expression. In addition, MdbHLH4 binds to the promoter of *MdCAX3L-2*, a Ca^{2+}/H^{+} exchanger (CAX) family gene, which negatively regulates apple cold tolerance, and promotes its expression. Under natural conditions, different stresses usually occur simultaneously. For example, the combined stresses of drought and cold induce shoot shriveling in apple trees. Li et al. (2023c) identified a zinc finger transcription factor, MhZAT10, which positively regulates the shoot-shriveling tolerance of apple rootstocks. DREB2A activates the expression of *MhZAT10* in response to drought, and MhZAT10 targets the downstream drought-tolerance gene *MhWRKY31* and the cold-tolerance genes *MhMYB88* and *MhMYB124*.

To cope with stresses, plants synthesize a variety of low-molecular mass compounds, including polyamines, soluble sugars, glycine betaine, and proline. Among these, soluble sugars are considered to be essential for maintaining cell membrane integrity, detoxifying reactive oxygen species (ROS), and adjusting osmotic potential under stress conditions. In addition, L-ascorbic acid (AsA) is an antioxidant implicated in abiotic stress tolerance and metabolism of ROS. Zhang et al. (2023c) reported the identification of 2 transcription factors, PtrABF4 and PtrABR1, being upstream transcription activators of PtrBAM3 in trifoliate orange (*Poncirus trifoliata* (L.) Raf.). PtrABF4 not only activates Ptr*ABR1* expression by binding to its promoter but also complexes with PtrABR1 to promote *PtrBAM3* expression, leading to enhanced drought tolerance. Liu et al. (2023a) identified a bZIP transcription factor from kiwifruit (*Actinidia eriantha* Benth.), AcePosF21, which interacts with AceMYB102 and activates *AceGGP3* expression, resulting in enhanced AsA production to resist cold stress.

High-temperature stress not only affects plant growth and development but also causes yield loss and deterioration of fruit quality. In banana (*Musa acuminata*), high temperatures (>24 °C) cause green ripening by inhibiting chlorophyll degradation. In a study by Luo et al. (2023), a key enzyme involved in chlorophyll degradation, MaNYC1, was reported to be degraded via the proteasome pathway under high temperature. In this process, a RING E3 ligase, MaNIP1, interacts with and ubiquitinates MaNYC1, leading to its proteasomal degradation.

Apple replant disease (ARD) is a soil-borne disease that severely hinders the renovation of old orchards because of its inhibition of the growth of young trees during replanting. *Fusarium* species are considered as the causal agents of ARD in apple-producing regions worldwide. To breed new apple rootstock varieties with ARD resistance, it is crucial to identify ARD resistance-related genes and elucidate the underlying regulatory networks. Liu et al. (2023c) revealed the role of the MdWRKY75-MdERF114-MdMYB8-MdPRX63 module in apple in response to *Fusarium solani* infection. In this module, MdERF114 promotes lignin deposition by regulating *MdPRX63* transcription, enhancing the resistance to *F. solani*. MdWRKY75 functions upstream of *MdERF114*. In addition, MdMYB8 interacts with MdERF114 and promotes its binding to the *MdPRX63* promoter.

Fruit ripening and other developmental processes

The fruit ripening process entails a series of remarkable alterations that consist of softening, accumulation of pigments, emission of aroma volatiles, and biosynthesis of characteristic nutriments (Giovannoni et al. 2017). Over the last 2 decades, there has been considerable progress in understanding the process of fruit ripening. In this Focus Issue, several update reviews summarize insights into post-transcriptional regulation (Wang et al. 2022) and epigenetic regulation of fruit ripening (Ji and Wang 2023), as well as the roles of biomolecules such as melatonin in modulating fruit ripening (Arabia et al. 2023). Excessive softening during the ripening of fleshy fruits can reduce quality and cause massive losses. Traditional plant breeding practiced in the last century has contributed significantly to the genetic improvement of fruit crops to combat these losses. However, fruit crops suffer from difficulties associated with classical breeding in terms of financial commitment, availability of land resources, and long generation time. For these reasons, genetic engineering may represent a valuable strategy to improve fruit crop species (Limera et al. 2017). The most recent discoveries in the field of molecular biology have led to the development of "new genomic techniques" (Nagamangala Kanchiswamy et al. 2015; Kanchiswamy et al. 2016). In this Focus Issue, 2 examples show how new genome tools can

be used to improve fruit softening (Shi et al. 2023) or enhance adventitious shoot regeneration in apple (Li et al. 2023a). With the improvement of these technologies, multigene genetic modification (cisgenesis or editing) can be achieved by a 1-time transformation without traditional crossbreeding.

Regulating ripening can extend the shelf-life of fruits during transportation and storage, reducing waste and improving economic outcomes. It is crucial to have a comprehensive understanding of the molecular mechanisms underlying the complex processes involved in fruit ripening. In this Focus Issue, He et al. (2023) resequenced a 4-generation pedigree consisting of 40 varieties derived from Pearl of Csaba (PC), a backbone parent for early ripening grapevine breeding, and found that the PC lines have lower nucleotide diversity. Importantly, a superior haplotype composed of alternative alleles, H1, is associated with early ripening. H1 encompasses a gene encoding a folate transporter with a missense mutation, which is specifically and highly expressed at the grapevine berry véraison period. Furthermore, D'Incà et al. (2023) reported the functional characterization of a grape NAC transcription factor, VviNAC60, which induces chlorophyll degradation and anthocyanin accumulation through the upregulation of STAY-GREEN PROTEIN 1 (VviSGR1) and VviMYBA1, respectively, with the latter being upregulated through a VviNAC60–VviNAC03 regulatory complex. Despite sharing a closer phylogenetic relationship with senescence-related homologs to the NAC transcription factor AtNAP, VviNAC60 complemented the nonripening (nor) mutant phenotype in tomato (*Solanum lycopersicum*), suggesting a dual role as an orchestrator for both ripening- and senescence-related processes. In apple, Li et al. (2023b) found that CYTOKININ RESPONSE FACTOR4 (MdCRF4) transcriptionally activates *1-AMINOCYCLOPROPANE-1-CARBOXYLIC ACID SYNTHASE 1 (MdACS1)* expression to enhance ethylene synthesis during ripening at normal basal Ca^{2+} levels. Ca^{2+} promotes Ca^{2+}/CaM-mediated phosphorylation of MdCRF4, leading to its ubiquitination and degradation by the E3 ligase MdXBAT31, thereby weakening *MdACS1* transcription and ultimately inhibiting ethylene biosynthesis during ripening. Meanwhile, other transcription factor, MdMADS5, is a transcriptional activator of the ethylene biosynthesis-related gene MdACS1, and Ca^{2+} promotes the MdCDPK7-mediated phosphorylation of MdMADS5, which results in the degradation of MdMADS5 via the 26S proteasome pathway. Furthermore, MdCDPK7 can also phosphorylate MdACO1, the key enzyme in ethylene synthesis, to degrade it and inhibit ethylene biosynthesis (Xu et al. 2023b). These findings provide insights into fruit ripening, which may lead to the development of strategies for extending the shelf-life of fruits.

Softening is an important aspect of the fruit ripening process. Ma et al. (2023) investigated the regulatory role of miRNA in peach fruit softening via mediating ethylene emission. Auxin-induced miRNA gene ppe-miR393a/b promotes ethylene biosynthesis via the ppe-miR393-PpTIR1-PpIAA13-PpACS1 module, resulting in peach fruit (*Prunus persica* L. Batsch) softening. The flesh of sweet cherry fruit (*Prunus avium* L.) is also susceptible to softening and rotting after harvest. Zhai et al. (2022) identified an ABA-mediated transcriptional cascade that controls the expression of cell wall modification-related genes, thus regulating fruit softening. C_2C_2-type transcription factors, PavDof2/6/15, bind directly to the promoters of cell wall modification-related genes. An auxin response factor, PavARF8, regulates the promoter activity of PavDof2/15 and PavNCED1, participating in ABA-mediated fruit softening. These findings establish a direct functional link between the ABA-PavARF8-PavDofs module and cell wall-modifying genes in mediating fruit softening.

Significant progress has also been made in other important aspects of fruit crop biology, such as embryogenesis in longan (*Dimocarpus longan*), female sterility in pomegranates (*Punica granatum*), and dwarfing in lemon (*Citrus limon* L. Burm.). Xu et al. (2023a) revealed that the microRNA, DlMIR408, targets DlNUDT23 to regulate riboflavin metabolism and RNA homeostasis, influencing cell division and differentiation in longan. Pomegranate male flowers show female sterility because of the abnormal development of ovules. Zhao et al. (2023) demonstrated that PgCRC, PgINO, and MADS-box transcription factors play critical roles in regulating floral organ development in female sterility in pomegranates. Dwarfism has a significant impact on crop yield, lodging resistance, planting density, and harvest index. Chu et al. (2023) showed that *ACS4* interacts with an ethylene response factor (ERF), CiERF3 in citrus. The CiACS4–CiERF3 complex regulates citrus plant height by altering the expression levels of 2 GA oxidase genes, *CiGA20ox1* and *CiGA20ox2*. The data elucidate the important role of *ACS* genes in regulating plant height.

Fruit acidity and sugar accumulation

Fruit acidity, measured as titratable acidity, is an important aspect of fruit quality, as it not only determines the degree of tart taste but also affects the perception of sweetness and aroma. Malic acid is the predominant organic acid in apple and many other fleshy fruits. Accumulation of malic acid in the vacuole of parenchyma cells in these fleshy fruits occurs via facilitated diffusion across the tonoplast, a process mediated by aluminum-activated malate transporters (ALMTs). *ALMT9* underlies a major genetic locus, *Ma*, for fruit acidity in apple. A naturally occurring mutation truncates the full-length ALMT9 (Ma1) by 84 amino acids to ma1, leading to low acidity in *ma1ma1* genotypes by decreasing malate transport into the vacuole (Li et al. 2020a). However, there are significant variations in fruit acidity in *Ma1Ma1* genotypes. In this Focus collection, Zheng et al. (2023) show that allelic variation in transcription factor MdMYB123 controls fruit malic acid content by differentially regulating the expression of *Ma1* and a gene encoding a P-type ATPase in the tonoplast via direct binding to their promoters, contributing to the difference in fruit acidity

among *Ma1Ma1* genotypes. In jujube (*Ziziphus jujuba*), *ALMT4*, a homolog of the apple *ALMT9*, is expressed at a lower level in the cultivated jujube than in its wild progenitor, sour jujube (*Z. jujuba* var. *spinosa*). The transcription factor WRKY7 binds to the promoter of *ALMT4*, activating its expression in sour jujube. However, the binding of WRKY7 to the promoter of *ALMT4* is weaker in cultivated jujube, conferring its low malic acid phenotype (Zhang et al. 2023a). In addition to genetic control, fruit acidity is also affected by environmental factors. Alabd et al. (2023) describe how salinity enhances malic acid accumulation in pear (*Pyrus* spp.) fruit. The expression of *ABRE-BINDING FACTOR 3* increases with salinity, activating the expression of transcription factor *WRKY44*, which in turn upregulates the expression of *ALMT9* for malic acid accumulation.

Sorbitol, a sugar alcohol present in small amount in many plant species, serves as a major photosynthate and transportable carbohydrate, along with sucrose, in apple and other pome and stone fruits in Rosaceae. Recent work indicates that sorbitol also acts as a signal regulating flower development, pollen tube growth, and disease tolerance in apple (Meng et al. 2018a, 2018b; Li et al. 2020b) and loquat (*Eriobotrya japonica*) (Xu et al. 2022). In this Focus collection, Meng et al. (2023) show that sucrose nonfermenting 1 (SNF1)-related protein kinase 1 (SnRK1) is involved in regulating the expression of both *SORBITOL DEHYDROGENASE 1* (*SDH1*) and *ALDOSE-6-PHOSPHATE REDUCTASE* (*A6PR*) in response to sorbitol via phosphorylation of transcription factor bZIP39. The findings integrate sorbitol signaling into the SnRK1-mediated sugar signaling network to modulate plant carbohydrate metabolism. As sorbitol is mainly converted to fructose by SDH, more than 80% of the carbon flux goes through fructose in apple and other sorbitol-transporting species in the Rosaceae, a unique feature of their carbohydrate metabolism (Li et al. 2018). A high-affinity fructose kinase, FRK2, plays an important role in fructose metabolism in apple, and its overexpression leads to lower fructose contents in leaves (Yang et al. 2018). Su et al. (2023) show that fruits of *FRK2* overexpression lines surprisingly accumulate more fructose. A skp1, cullin, F-box (SCF) E3 ubiquitin ligase, calcyclin-binding protein (CacyBP) interacts with and ubiquitinates FRK2 to enhance its degradation via the 26S proteasome, which lowers the FRK protein level and enzyme activity for fructose accumulation in the transgenic fruit. This provides a posttranslational mechanism for regulating fructose in sorbitol-transporting species. In addition to fructose, sucrose accumulation contributes significantly to total soluble sugars in apple. Zhang et al. (2023b) show that sugars will eventually be exported transporter 9b (SWEET9b) is involved in sucrose accumulation in apple, probably via mediating sucrose unloading from sieve elements and the surrounding parenchyma cells in the fruit vascular tissue. Transcription factor WRKY9 activates *SWEET9b* expression by binding to its promoter in response to ABA. MdWRKY9 also interacts with 2 other transcription factors, MdbZIP23 and MdbZIP46, at the protein and DNA levels to enhance its regulatory effect on *MdSWEET9b* expression. Fang et al. (2023) demonstrated that SUCROSE SYNTHASE 5 (SUS5) and SWEET6 mediate sucrose metabolism and fructose accumulation in citrus fruit. A homolog of transcription factor ZINC FINGER OF ARABIDOPSIS THALIANA 5 enhances sucrose metabolism and fructose transport by activating the expression of both *CitSUS5* and *CitSWEET6* in citrus. These findings suggest that both sugar metabolism and SWEET-mediated sugar transport play important roles in sugar accumulation in fleshy fruits.

Specialized metabolites in fruit

Plants have evolved to produce an astonishing array of specialized metabolites that provide advantageous adaptations to their environments for protection and pollination (Pichersky and Lewinsohn 2011). In addition to aiding defense against biotic and abiotic stresses, these specialized metabolites impart the colors and volatiles to fruits that attract seed dispersers, and ultimately to us, as consumers.

Over the last 2 decades, there has been considerable progress in understanding the synthesis of specialized metabolites and its regulation. For anthocyanin, while the most specific control is by the MYB-bHLH-WD40 (MBW) transcriptional complex (Albert et al. 2014), increasingly, we see evidence for posttranscriptional and posttranslational nuances that influence the function of the MBW complex. In this Focus Issue, Yao et al. (2023) describe how the signaling molecule hydrogen sulfide (H_2S) inhibits anthocyanin production in red-skinned pears. In this instance, the function of H_2S is to mediate a persulfidation of PyMYB10, which alters its ability to interact with other MYBs and, crucially, its ability to activate key anthocyanin biosynthesis pathway genes, resulting in a reduced capacity for anthocyanin production. Anthocyanin production is also controlled by environmental influences (Jaakola 2013). In sweet cherry, Wang et al. (2023b) show that light stimulates the expression of 2 BBX proteins, PavBBX6/9, as well as the induction of ABA. It appears that PavBBX9/9 upregulates 9-CIS-EPOXYCAROTENOID DIOXYGENASE, PavNCED1, leading to increased ABA, which, in turn, increases the expression of PavBBX6/9. This feedback loop is further augmented by the ability of PavBBX6/9 to directly bind to and activate the promoter of the final gene in the anthocyanin pathway, *UDP GLUCOSE-FLAVONOID-3-O GLUCOSYLTRANSFERASE* (*UFGT*), and so drive anthocyanin synthesis by light- and ABA-integrated signals. The relationship between anthocyanin synthesis and phytohormones has been established for both nonclimacteric fruits, such as ABA in the case of sweet cherry, and ethylene in climacteric fruits, such as in pear and apple. In pear, it has been shown that the ethylene response factor, ERF3, forms a complex with PyMYB114 and PybHLH3 to increase anthocyanin in pear skin (Yao et al. 2017). New research in pear by Sun et al. (2023) shows how the ERF3-MYB114-bHLH3 complex is broken to inhibit anthocyanin production. The ERFs, PyERF4.1/4.2, are

transcriptionally activated by the anthocyanin-regulating MYB, PyMYB114, and these ERFs then bind with the ERF3-MYB114-bHLH3 complex at the EAR motif of ERF3, preventing the complex from binding with anthocyanin pathway genes and leading to reduced anthocyanin accumulation.

Fruit waxes are important for protecting fruits against pathogen attacks and provide a water-permeable barrier. In apple, this barrier is useful for long-term storage. Zhang et al. (2023d) describe a new function for the apple small ubiquitin-like modifier (SUMO) E3 ligase, SAP AND MIZ1 DOMAIN CONTAINING LIGASE1 (MdSIZ1), in regulating wax accumulation. They show how MdSIZ1 mediates the SUMO modification of the MYB transcription factor, MdMYB30, which has previously been shown to regulate wax biosynthesis (Zhang et al. 2019). This MYB is then able to drive expression of β-KETOACYL-COA SYNTHASE 1, MdKCS1, which provides a key rate-limiting step in fatty acid elongation as part of wax biosynthesis.

While waxes are beneficial for fruits, the lignification that results in stone cells is not. Xue et al. (2023) identify a MYB transcription factor from *Pyrus bretschneideri*, PbrMYB24, which directly activates secondary cell wall enzymes involved in lignin and cellulose biosynthesis. This work also demonstrated the ability of PbrMYB24 to activate 2 previously identified positive regulators of lignification, NAC STONE CELL PROMOTING FACTOR (PbrNSC) and PbrMYB169 (Xue et al. 2019; Wang et al. 2021). Conversely, both these genes can activate PbrMYB24, suggesting some feedback mechanism and a central role for PbrMYB24 (Oliveira 2023). Research into another unwanted phenomenon, fruit browning, has provided a new mechanism in apple (Wang et al. 2023a). In this study, the authors show that a laccase gene, MdLAC7, induces peel browning under dark conditions, using phenolics and flavonoids as oxidation substrates. Furthermore, this process is positively regulated by the WRKY transcription factor, MdWRKY31, which drives MdLAC7 expression. However, in the light, this process is prevented by the presence of ELONGATED HYPOCOTYL 5 (MdHY5), which binds to the promoter of MdWRKY31, preventing its expression and the activation of MdLAC7. This alternative mechanism to the well-studied polyphenol oxidases provides a MdHY5-MdWRKY31-MdLAC7 complex that mediates peel browning, which may be offset by light exposure, a consideration for the practice of apple bagging.

Outlook and acknowledgments

The combined efforts of the editorial team over the last 12 mo have culminated in this Focus Issue. We thank all the authors and reviewers for their valuable contributions. These Updates and Research Articles, while did not cover all topics of fruit biology, shed new light on various aspects of fruit crop biology and highlight the significant progress that is being made in fruit crop research. We look forward to exciting future progress, building on technological advancements in genomics, plant transformation, molecular biology, biochemistry, molecular breeding, and genome editing on this group of economically important plants. Finally, we hope you enjoy reading the papers as much as we have enjoyed assembling them.

Conflict of interest statement. None declared.

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