Plant Physiology®

Fruit crops combating drought: Physiological responses and regulatory pathways

Xiaomin Liu (ID),[†] Tengteng Gao (ID),[†] Changhai Liu (ID), Ke Mao (ID), Xiaoqing Gong, Chao Li (ID)*
and Fengwang Ma (ID)*

State Key Laboratory of Crop Stress Biology for Arid Areas/Shaanxi Key Laboratory of Apple, College of Horticulture, Northwest A&F University, Yangling 712100, Shaanxi, China

*Author for correspondence: lc453@163.com (C.L.), fwm64@nwsuaf.edu.cn (F.M.)
[†]These authors contributed equally to this work.
The author responsible for distribution of materials integral to the findings presented in this article in accordance with the policy described in the Instructions for Authors (https://academic.oup.com/plphys/pages/general-instructions) is Fengwang Ma (fwm64@sina.com).

Abstract

Drought is a common stress in agricultural production. Thus, it is imperative to understand how fruit crops respond to drought and to develop drought-tolerant varieties. This paper provides an overview of the effects of drought on the vegetative and reproductive growth of fruits. We summarize the empirical studies that have assessed the physiological and molecular mechanisms of the drought response in fruit crops. This review focuses on the roles of calcium (Ca^{2+}) signaling, abscisic acid (ABA), reactive oxygen species signaling, and protein phosphorylation underlying the early drought response in plants. We review the resulting downstream ABA-dependent and ABA-independent transcriptional regulation in fruit crops under drought stress. Moreover, we highlight the positive and negative regulatory mechanisms of microRNAs in the drought response of fruit crops. Lastly, strategies (including breeding and agricultural practices) to improve the drought resistance of fruit crops are outlined.

Introduction

Fruits are essential to a balanced diet because they provide a natural source of phytochemicals, nutrients, and dietary fiber (Sabbadini et al. 2021). An adequate fruit intake alleviates micronutrient deficiencies, and the dietary polyphenols in some fruits reduce inflammation in the short or long term (Joseph et al. 2016; McMullin et al. 2019). However, fruit crops often suffer drought damage (Faghih et al. 2021). All regions of the world are affected by drought due to climate change, leading to fruit crop losses (Rachappanavar et al. 2022). Water scarcity is common in many fruit-producing areas worldwide, especially in China, the largest fruit producer. Fruit crops are commonly planted on slopes, where drought is more prominent. Therefore, it is necessary to understand the mechanisms by which fruit crops respond to drought and to intervene with targeted biotechnological approaches to ensure viable fruit production.

Plant roots are in direct contact with the soil and absorb most of the water required by plants (Lobet and Draye 2013). The characteristics and dynamics of plant roots, including the root angle, surface area, average diameter, length, number of tips and forks, weight, volume, and density, allow plants to respond to drought and cope with the early stages of drought stress (Hu and Xiong 2014). In addition, the roots' anatomical features, such as the number, size, and morphology of cells, the thickness of the outer cell wall, and the cell density, can be adapted under drought stress to enhance water and nutrient uptake and provide mechanical strength to the root system (Morris et al. 2017; Lynch 2019).

Leaves are the main location of photosynthesis and the organ with the largest area exposed to the environment. The keratinization of the leaf surface, a reduction in leaf area, and the thickening of the palisade tissue and leaves are some changes occurring in plants under drought stress (Fang and Xiong 2015). Moreover, drought results in the

ADVANCES

- Fruit crops adapt to drought stress at the physiological level via osmotic regulation, balancing the production and removal of reactive oxygen species, hormonal changes, secondary metabolism, and autophagy.

- Drought-related transcription factors (ABA-dependent and ABA-independent) are initiated by drought signals, and various microRNAs positively and negatively regulate drought tolerance in fruit crops.

- Strategies to reduce drought stress in fruit crops include selecting drought-tolerant varieties and genes, grafting onto drought-tolerant rootstocks, transgenic and polyploid breeding, using exogenous plant growth regulators and biostimulants, and water-deficit irrigation.

closure of stomata (the organs through which leaves exchange gases with their surroundings, formed by paired guard cells), leading to a substantial reduction in net photosynthetic rates (Daszkowska-Golec and Szarejko 2013).

Fruit is the only or primary product harvested from fruit crops. Flower bud differentiation, fruit set, and fruit development largely determine the yield and quality of fruit crops. Flower bud differentiation is triggered by moderate water-deficit stress. A flowering model for lemon [*Citrus limon* (L.) Burm. f.] buds was proposed to understand the mechanism of water deficit-induced flowering (Li et al. 2017a). The mechanism of flower bud differentiation in response to drought in perennial woody fruit crops remains unclear (see Outstanding Questions). However, drought stress often results in numerous aborted fruits, substantially reducing fruit setting (Liu et al. 2013). Fruit development occurs after successful flower bud differentiation and fruit set. The size, quality, and aroma of fruit determine fruit quality. The size of highbush blueberries (*Vaccinium corymbosum*) decreased or did not change significantly under drought stress (Lobos et al. 2018). Fruit quality is primarily determined by the sugar content, acid content, and its ratio. Many studies reported that moderate drought stress improved fruit quality (e.g. increasing the sugar and acid content) in peaches (*Prunus persica* L. Batsch) (Miras-Avalos et al. 2013). In contrast, the sugar content of Rangpur lime (*Citrus limonia* Osbeck) (a drought-tolerant citrus rootstock) was decreased by severe water deficit (Silva et al. 2023). The aroma of all fleshy fruits comes from various volatiles, and a favorable aroma increases fruit consumption. Beneficial effects of water deficit on fruit aroma have been reported in different species. A study on grapes (*Vitis vinifera* L.) found that drought stress caused an increase in the contents of volatile organic compounds, resulting in complex aromas that improved wine quality (Balint and Reynolds 2017).

This review summarizes the physiological and molecular mechanisms by which fruit crops cope with drought stress and suggest strategies to enhance the drought resistance of fruit crops.

Physiological mechanisms to cope with drought

Osmotic adjustment

Osmotic adjustment refers to the accumulation of various inorganic or organic substances when the cell's water potential decreases, thereby reducing the osmotic potential. The substances involved in osmotic adjustment in fruit crops include inorganic ions and organic solutes (such as soluble sugars, alkaloids, organic acids, and polyols).

Sorbitol is a major photosynthate and a soluble transport carbohydrate in Rosaceae fruit crops. In response to drought, all sorbitol-synthesizing pome and stone fruits accumulate sorbitol in the leaves, a critical aspect of osmotic adjustment. In the sorbitol biosynthetic process in the source leaves, glucose-6-phosphate is catalyzed by aldose-6-phosphate reductase (A6PR), also called sorbitol-6-phosphate dehydrogenase, to generate sorbitol-6-phosphate, which is converted to sorbitol via sorbitol-6-phosphate phosphatase (Negm and Loescher 1981). The antisense suppression of *A6PR* decreased the transcript level and activity of A6PR in mature leaves (Cheng et al. 2005) and reduced the sorbitol concentration in the source leaves of apple (*Malus domestica*) trees (Li et al. 2018a). In response to short-term water deficits, the activity of A6PR and the expression of *MdA6PR* were increased to accumulate sorbitol (Yang et al. 2019). Water stress induced sorbitol accumulation in drought-sensitive 'NaganoFuji' and drought-insensitive 'QinGuan' apples and peaches (Lo Bianco et al. 2000). The leaves of 'QinGuan' apples with higher sorbitol concentrations wilted more slowly than those of 'NaganoFuji' apples (Wu et al. 2014b). In addition to being a key osmoprotectant in response to drought, sorbitol also acts as a signal regulating stamen development (Meng et al. 2018a), pollen tube growth (Li et al. 2020a), and resistance to *Alternaria alternata* (Meng et al. 2018b) in *M. domestica*.

Reactive oxygen species

When plants are exposed to drought stress, the dynamic balance between producing and removing reactive oxygen species (ROS) is disrupted. Enzymatic and nonenzymatic reactions are activated in plants to remove excessive ROS (Miller et al. 2010). ROS-scavenging enzymes include ascorbate peroxidase (APX), catalase (CAT), superoxide dismutase (SOD), and glutathione peroxidase. The nonenzymatic defense system is comprised of several nonenzymatic and low-molecular weight antioxidants, such as proline (Pro), ascorbic acid (AsA), carotenoids, glutathione (GSH), cytochrome f (Cytf), a-tocopherol (vitamin E), flavanones, and anthocyanins.

Phytohormones

Phytohormones play a vital role in combating drought stress in fruit crops. Endogenous abscisic acid (ABA) levels increase as fruit crops sense the onset of drought stress. The accumulation of ABA activates downstream signals, and the main effects are stomatal closure and the prevention of stomatal opening, thereby limiting excessive water loss in plants (Kalladan et al. 2017). Crosstalk between ABA and other hormones under drought conditions has been extensively studied in recent years. For example, Xu et al. (2022a) found that auxin and ABA antagonistically regulate AsA accumulation to scavenge ROS. Sun et al. (2022) found that ABA and jasmonic acid (JA) have synergistic effects on the resistance to dehydration stress in apples (*M. domestica*). Nolan et al. (2019) found that the brassinosteroid hormone antagonized the signal components of the ABA pathway to regulate the drought response. In addition, drought reduces the contents of cytokinins (CTK) and auxins (AUX/IAA), stimulating ethylene (ET) production (Rowe et al. 2016). When water is scarce, salicylic acid (SA) stimulates the production of ROS to close stomata (Miura et al. 2013). In general, there are fewer growth stimulators and more growth inhibitors in fruit crops under drought conditions.

Secondary metabolites

Various secondary metabolic pathways produce small organic compounds which are categorized as secondary metabolites. Extensive studies have shown that higher concentrations of secondary metabolites were accumulated in fruit crops exposed to drought stress. Recently, melatonin (MT), an indole substance and a potent, naturally occurring antioxidant, was found to play a vital role in the drought resistance in fruit crops (Fig. 1). N-acetylserotonin-O-methyltransferase (ASMT) and serotonin N-acetyltransferase (SNAT) are key enzymes in the synthetic pathway of MT in plants (Park et al. 2013; Wang et al. 2017a). Evidence indicates that the endogenous MT content is elevated by applying exogenous MT (Liang et al. 2018b; Wang et al. 2021a) and the overexpression of *ASMT* (Zhou et al. 2022) and *SNAT* (Wang et al. 2017a) under normal and drought conditions in fruit crops. Under drought, MT protects chlorophyll from breakdown by decreasing the gene expression related to chlorophyll degradation, such as pheophorbide a oxygenase (*PAO*) in apple (Wang et al. 2013b) and chlorophyllase (*CHLASE*) in Chinese hickory (*Carya cathayensis*) (Sharma et al. 2020). Drought-induced leaf senescence in apple is suppressed by chlorophyll degradation and the upregulation of the senescence-associated gene 12 (*SAG12*) (Wang et al. 2013b). The chlorophyll content was elevated in apple (Liang et al. 2018b), kiwifruit (*Actinidia chinensis*) (Liang et al. 2019), grape (Meng et al. 2014), *C. cathayensis* (Sharma et al. 2020), and loquat (*Eriobotrya japonica* Lindl.) (Wang et al. 2021a) by applying MT in drought conditions. When chlorophyll is exposed to light, the photosynthetic apparatus, including photosystem I (PSI) and photosystem II (PSII) convert light energy into chemical energy. MT increases the quantum yield of PSII

in above fruit crops (apple, kiwifruit, grape, *C. cathayensis*, and loquat). Nevertheless, the effect of MT on PSI in fruit crops under drought requires more research. The antioxidant power of MT may protect the integrity of the photosynthetic apparatus, which can be damaged by large amounts of ROS produced during drought. MT removes ROS in two species of lime plants ["Persian lime" (*Citrus latifolia* Tanaka) and "Mexican lime" (*Citrus aurantifolia* (Christm) Swingle)] (Jafari et al. 2022), apple (Liang et al. 2018b), and grape (Meng et al. 2014) and enhances the activity of SOD, CAT, and APX and the expression of genes encoding these antioxidant enzymes under drought. MT also regulates the nonenzymatic antioxidant system. The ratios of AsA/dehydroascorbate and GSH/GSSG (oxidized glutathione) in apple, the contents of AsA and GSH in grape, and the activity of glutathione reductase are increased by the application of MT during a drought. Applying MT also increased the contents of other secondary metabolites with high antioxidant capacity, such as essential oil, phenolic, and flavonoid compounds in citrus (Jafari and Shahsavar 2021) and *C. cathayensis* (Sharma et al. 2020). Furthermore, the stomatal properties (number, stomatal length, width, etc.) are improved by applying MT to apple (Zhou et al. 2022) and grape (Meng et al. 2014), possibly due to a decrease in the ABA content. Under drought, MT also raises the contents of IAA, JA, and CTK by regulating the expression of biosynthetic genes to improve drought resistance in loquat (Wang et al. 2021a) and *C. cathayensis* (Sharma et al. 2020). Conversely, the IAA levels of transgenic *MzASMT1* Arabidopsis (*Arabidopsis thaliana*) lines were lower than that of the wild type, which may be because IAA and MT share the same precursor (Zuo et al. 2014).

In addition, dopamine, a natural product of the catecholamine pathway, also has a strong antioxidative capacity (Kulma and Szopa 2007). Tyrosine decarboxylase synthesizes tyramine from tyrosine, which is used to produce dopamine (Świędrych et al. 2004). The apple dopamine content is substantially increased by the overexpression of *MdTYDC*, and the enhanced photosynthetic performance, lower water loss rate, and higher ABA levels may be attributed to the increased dopamine content in transgenic *MdTYDC*-overexpression apples under short- (Gao et al. 2021) and long-term (Wang et al. 2021b) moderate drought conditions.

Autophagy

Autophagy, a subcellular degradation and recycling pathway, removes damaged organelles or proteins under drought stress. Autophagy activity can be triggered by drought in apple (Wang et al. 2014, 2017b) and peach (Wang et al. 2019). AUTOPHAGY-RELATED (ATG) proteins are part of this mechanism. Under drought, CONSTITUTIVELY STRESSED 1 protein (COST1), a plant-specific protein, is ubiquitinated and degraded by autophagy and the 26S proteasome in Arabidopsis. Subsequently, ATG8 is released, and autophagy is activated (Bao et al. 2020). ATG8 is conjugated with phosphatidylethanolamine (PE) by two ubiquitin ligation-like pathways (such as ATG5 and ATG7) to form ATG-PE, which is involved in autophagosome formation and cargo
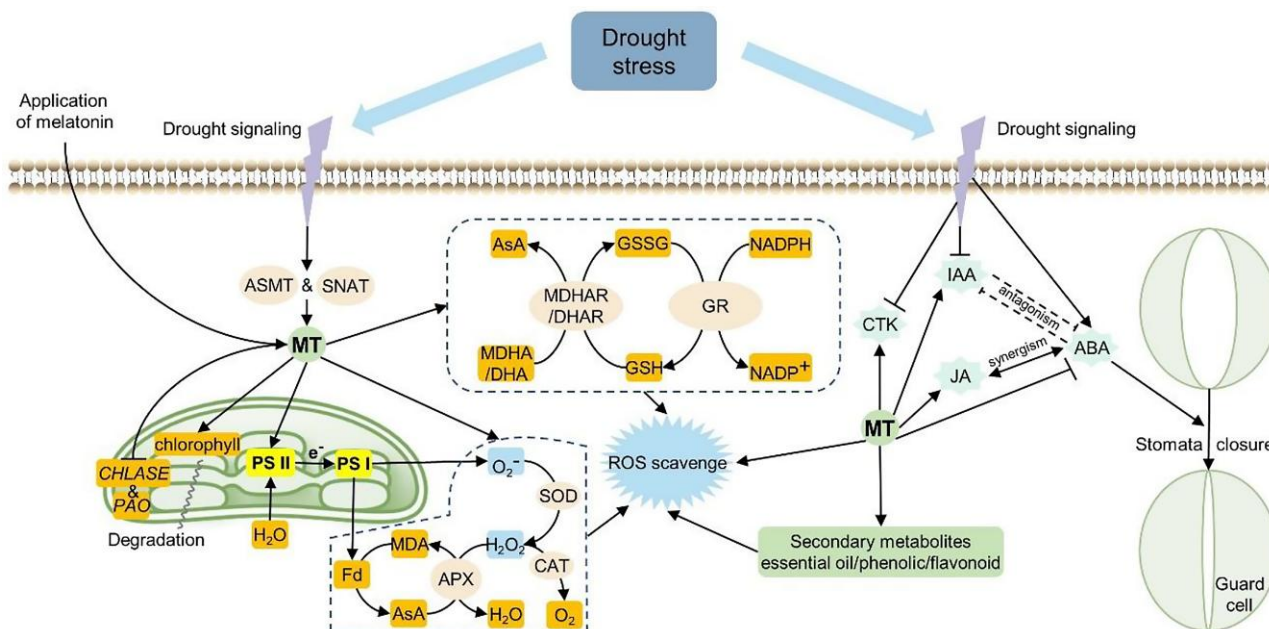
Figure 1. The role of melatonin in the drought stress response of fruit crops. Under drought, the MT content is enhanced by the application of exogenous MT and the overexpression of ASMT and SNAT. MT protects PSII and reduces the regulation of chlorophyll by repressing the expression of *CHLASE* and *PAO*. MT not only acts as a direct scavenger of ROS but also regulates secondary metabolites, enzymatic and nonenzymatic systems to remove ROS. MT also showed crosstalk with CTK, IAA, and JA to response drought. Furthermore, MT decreases ABA content to promote stomata closure. The solid arrows refer to direct effects, blocked arrows refer to inhibition. MT, melatonin; ASMT, N-acetylserotonin-O-methyltransferase; SNAT, serotonin N-acetyltransferase; CHLASE, chlorophyllase; PAO, pheophorbide a oxygenase; PSI/II, photosystem I/II; Fd, ferredoxin; MDA, mono-dehydroascorbate; AsA, reduced ascorbate; APX, ascorbate peroxidase; CAT, catalase; SOD, superoxide dismutase; ROS, reactive oxygen species; MDHA/DHA, monodehydroascorbate/dehydroascorbate; MDHAR/DHAR, monodehydroascorbate reductase/dehydroascorbate reductase; GSSG, oxidized glutathione; GSH, reduced glutathione; GR, glutathione reductase; NADPH/NADP, reduced nicotinamide adenine dinucleotide phosphate/nicotinamide adenine dinucleotide phosphate; CTK, cytokinin; JA, jasmonic acid; IAA, indole-3-acetic acid; ABA, abscisic acid.

recruitment (Chung et al. 2010). The autophagic activity is enhanced by the overexpression of *MdATG8i*, which improves the osmoregulation ability, water-use efficiency, and photosynthetic capacity of *MdATG8i*-OE apple plants under long-term moderate drought stress (Jia et al. 2021b). The overexpression of *MdATG5a* also promotes autophagic activity under drought stress, thus regulating osmotic adjustments by the mobilization of starch (Jia et al. 2021a). In addition, the antioxidant capacity is substantially elevated in transgenic *MdATG18a*-overexpression apple lines, which is likely due to the higher frequency of autophagy (Sun et al. 2018). Plant hormone signaling is modulated by autophagy during drought stress, such as ABA, CTK, ET, SA, and brassinosteroids (Liao and Bassham 2020). A 1-μM 24-epibrassinolide (a highly active synthetic analog of the brassinosteroids) treatment alleviated drought stress-induced damage and reduced the number of autophagosomes in peach (*P. persicae* L.) leaves (Wang et al. 2019). The above studies represent the research progress of autophagy in fruit crops under drought in recent years. Readers are referred to reviews of the function and regulation of autophagy in plants under drought (Tang and Bassham 2022).

Molecular mechanisms of drought response

This section reviews recent advances in elucidating the sensing and signaling mechanisms, downstream transcriptional regulation, and microRNA (miRNA) response pathways of drought stress in plants, mainly fruit crops.

Sensing and signaling mechanisms

Studies on the sensing and signaling mechanisms of drought stress have mainly focused on model plants. Insufficient water is one reason for hyperosmotic stress in plants; thus, drought may first be perceived as a decline in the osmotic potential (Zhu 2016). Hyperosmotic stress is sensed by the plasma membrane-localized Ca^{2+} channels OSCA1 (osmolality-sensing ion channel 1) or OSCA1.2 in Arabidopsis (Yuan et al. 2014; Liu et al. 2018) (Fig. 2). Under hypertonic conditions, the OSCA ion channels open due to reduced cell turgor pressure, causing the transport of Ca^{2+} into cells (Liu et al. 2018; Maity et al. 2019). Stress-specific signal transduction is triggered by the perception of hypertonic conditions. This process includes Ca^{2+}, ABA, ROS, H^+ (pH), lipids, nitric oxide (NO), RNA, post-translational modifications of proteins, small peptides, and
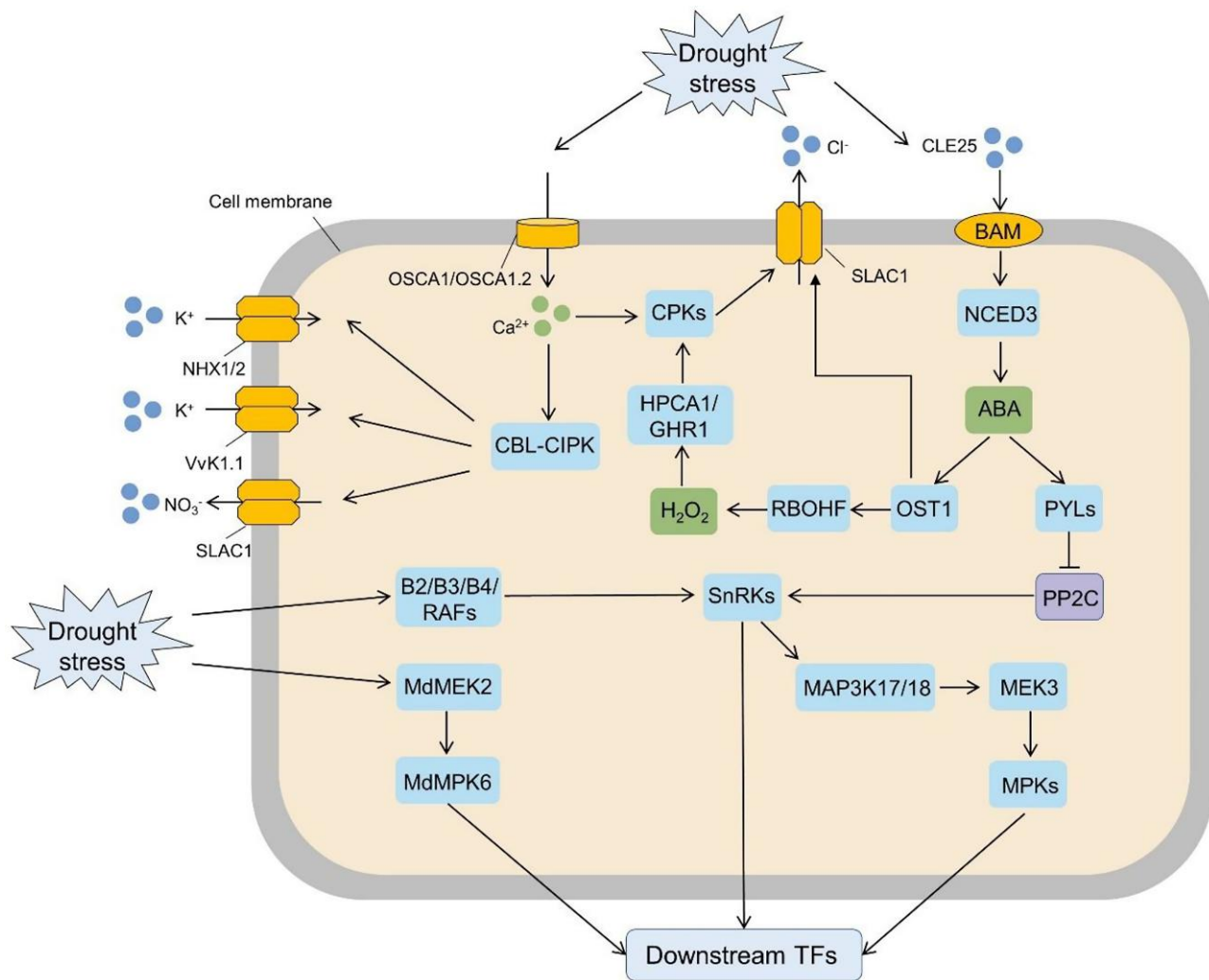
Figure 2. The sensing and signaling mechanisms of drought stress in plants. Drought is likely perceived as a decline in osmotic potential, which is sensed by the Ca^{2+} channel OSCA1 or OSCA1.2, causing the transport of Ca^{2+} into cells. The downstream signaling responses are thus mediated. The drought signal transduction network highlights the roles of Ca^{2+} signaling, ABA, ROS signaling, and protein phosphorylation. The solid arrows refer to direct effects, blocked arrows refer to inhibition, shapes on the cell membrane refer to the sensors. Cl^-, chloride ion; CLE25, CLAVATA3/ EMBRYO-SURROUNDING REGION-RELATED 25; BAM, BARELY ANY MERISTEM; OSCA1/OSCA1.2, osmolality-sensing ion channel 1/osmolality-sensing ion channel 1.2; SLAC1, slow anion channel-associated 1; Ca^{2+}, calcium ion; CPKs, calcium-dependent protein kinases; NCED3, 9-cis-epoxycarotenoid dioxygenase 3; K^+, potassium ion; NHX1/2, tonoplast-localized K^+/H^+ exchangers; VvK1.1, inward shaker K^+ channel (the counterpart of *Arabidopsis* AKT1); NO_3^-, nitrate ion; CBL–CIPK, calcineurin B-like-interacting protein kinase; HPCA1/GHR1, HYDROGEN PEROXIDE-INDUCED Ca^{2+} INCREASE 1/GUARD CELL HYDROGEN PEROXIDE-RESISTANT1; ABA, abscisic acid; H_2O_2, hydrogen peroxide; RBOHF, one of the isoforms belonging to the respiratory burst oxidase homologs (RBOHs); OST1, OPEN STOMATA 1; PYLs, pyrabactin resistance (PYR)/PYR1-like receptors; B2/B3/B4/RAFs, B2/B3/B4 clades of Raf-like kinases; SnRKs, the members of sucrose nonfermenting 1 (SNF1)-related protein kinases; PP2C, type 2C protein phosphatase; MdMEK2, mitogen-activated protein kinase kinase 2; MAP3K17/18, mitogen-activated protein kinase kinase kinase 17/18; MEK3, mitogen-activated protein kinase kinase 3; MdMPK6, mitogen-activated protein kinase 6; MPKs, mitogen-activated protein kinases; TFs, transcription factors.

physical signals (Gong et al. 2020; Lamers et al. 2020; Zhang et al. 2022a). Here, we focus on Ca^{2+} signaling, ABA, ROS signaling, and protein phosphorylation, which are critical for drought signal transduction.

Calcium-dependent protein kinases and calcineurin B-like-interacting protein kinases (CBLs–CIPKs) may be activated by the Ca^{2+} signal, stimulating the slow anion

channel-associated 1 (SLAC1) S-type anion channel (Maierhofer et al. 2014; Brandt et al. 2015), which is responsible for the efflux of anions (Cl^- and NO_3^-). Drought signals initiated by hyperosmotic stress are divided into ABA-independent and ABA-dependent types. Some B2/B3/ B4 clades of Raf-like kinases are activated independently of ABA in response to drought stress and then activate

SnRK2s [the members of sucrose nonfermenting 1 (SNF1)-related protein kinases] (Katsuta et al. 2020). Under hyperosmotic stress, ABA binds to pyrabactin resistance (PYR)/PYR1-like receptors, which then physically interact with and inhibit type 2C protein phosphatase, resulting in the activation of SnRK2s (Ma et al. 2009; Park et al. 2009; Chen et al. 2020a). The activated SnRK2s then phosphorylate downstream effector proteins, such as SLAC1 (Brandt et al. 2015), transcription factors (TFs) (Zhu 2016), and RBOHF [one of the isoforms belonging to the respiratory burst oxidase homologs (RBOHs)] (Drerup et al. 2013). Moreover, ABA and water stress can induce the expression of OPEN STOMATA 1 (OST1), a kinase located in guard cells and involved in ABA-induced stomatal closure (Belin et al. 2006; Yoshida et al. 2015). The primary function of OST1 is kinase regulation of anion channels in guard cell ABA signaling (Assmann and Jegla 2016). OST1 has been characterized in Arabidopsis (Belin et al. 2006), tomato (Solanum lycopersicum) (Burger 2022), cabbage (Brassica oleracea) (Wang et al. 2013a), maize (Zea mays) (Wu et al. 2019), poplar (Populus euphratica) (Rao et al. 2023), and rice (Oryza sativa) (Zhang et al. 2023). In addition to phosphorylating SLAC1 at Ser-120 to activate the anion channel (Geiger et al. 2009) and phosphorylating the microtubule-associated protein SPIRAL1 (SPR1) at Ser-6 to facilitate microtubule disassembly (Wang et al. 2022b), OST1 also targets RBOHF to generate ROS under osmotic stress (Han et al. 2019). H_2O_2 is likely sensed by GUARD CELL HYDROGEN PEROXIDE-RESISTANT1 (GHR1) (Hua et al. 2012) and the leucine-rich repeat receptor kinase HYDROGEN PEROXIDE-INDUCED Ca^{2+} INCREASE 1 (HPCA1) (Wu et al. 2020) to generate Ca^{2+} signals. Thousands of different mitogen-activated protein kinase (MPK/MAPK) modules can be combined due to the many family members in the plant MAPK pathway. The kinase cascades consisting of MAPK, MAPK kinase (MAP2K/MKK/MEK), and MAPK kinase kinases (MAPKKK/MEKK/MAP3K) are often involved in osmotic stress signal transduction. For example, the modules of MAP3K17/18–MKK3–MPK1/2/7/14 cascades respond to ABA downstream of SnRK2s during drought stress responses in plants (Danquah et al. 2015; de Zelicourt et al. 2016). In addition, a small peptide called CLAVATA3/EMBRYO-SURROUNDING REGION-RELATED 25 (CLE25), a long-distance messenger from roots to shoots, was recently discovered. The drought signal caused CLE25 to form CLE25 peptide in roots, which was transferred to the vasculature and the leaves. After CLE25 was bound to its receptor proteins BARELY ANY MERISTEM (BAM), it caused the expression of 9-cis-epoxycarotenoid dioxygenase 3 (NCED3), a gene encoding the key ABA biosynthetic enzyme, increasing the ABA concentration and reducing stomatal opening in response to dehydration stress (Takahashi et al. 2018).

Recently, several groups have independently reported the early response of fruit crops to drought signals (Fig. 2). Under drought stress, MdPYL9 interacts with MdPP2CAs in ABA-dependent and ABA-independent pathways (Yang et al. 2022b), suggesting that a nonABA signal may drive the interaction between PYL9 and PP2CAs in response to drought signals in apple plants. Water-deficit stress also substantially increases MdMPK6 activity, and the constitutively active form of MdMEK2-activated MdMPK6 then elicits downstream transcriptional regulatory responses (Shan et al. 2021). It is well known that ABA promotes stomatal closure under drought stress (Brodribb and McAdam 2013). Song et al. (2018) reported that CBL–CIPK modules activated the tonoplast-localized K^+/H^+ exchangers (NHX1 and NHX2) to promote vacuolar K^+ accumulation, negatively regulating ABA-mediated stomatal closure. Similarly, the CBL1–CIPK23 network activates an inward shaker K^+ channel (VvK1.1, the counterpart of Arabidopsis AKT1) in grape berries under drought stress (Cuellar et al. 2010).

Transcriptional regulation

Following the sensing of drought stress cues, downstream transcriptional regulatory responses are triggered in fruit crops. TFs are the major regulators of gene expression and play a pivotal role in the drought response via ABA-dependent and ABA-independent pathways (Fig. 3).

In ABA-dependent regulation, ABSCISIC ACID-INSENSITIVE5 is a vital transcription factor in the drought stress response. In apple, the expression of MdABI5 is triggered by ABA or drought signaling, enhancing the expression levels of ABA-responsive genes EARLY METHIONINE-LABELED6 (MdEM6) and RESPONSIVE TO DESICCATION29A (MdRD29A) by directly binding to their promoters, which in turn increases the ABA contents to enhance drought resistance. Meanwhile, TEOSINTE BRANCHED 1/CYCLOIDEA/PCF (MdTCP46), which is repressed by ABA or drought signaling, interacts with and inhibits MdABI5 to regulate drought tolerance negatively (Liu et al. 2022). Drought was found to induce the expression of MdAREB2, which then targets and induces the expression of amylase genes (MdAMY1, MdAMY3, MdBAM1, and MdBAM3), Suc uptake transporter (MdSUT2) and tonoplast monosaccharide transporter (MdTMT1). This signal subsequently activates the expression of MdSUT2, eventually leading to the accumulation of soluble sugar to influence drought tolerance (Ma et al. 2017). This regulatory pathway sheds light on why drought promotes fruit quality. In grape, the expressions of two lignin biosynthetic genes [peroxidase4 (VvPRX4) and (VvPRX72)] were increased by overexpressing VlbZIP30, a positive regulator of dehydration tolerance through the ABA core signaling pathway (Tu et al. 2018), thus promoting the deposition of lignin in grapevine stems under drought. In the meanwhile, VlbZIP30 also bound the promoter of VvNAC17 (drought-responsive gene) and VvPRX N1 in grapevine leaves, improving drought resistance (Tu et al. 2020). ABA plays a key role in plant drought tolerance and regulates the expression of most target genes via the ABA-responsive element (ABRE) and the ABRE binding protein/ABRE binding factor (AREB/ABF) TFs. Zhang et al. (2022c) found that the PtrABF4–PtrABR1 TF complex upregulated the β-amylase gene (BAM3) expression in trifoliate orange [Poncirus trifoliata (L.) Raf.], promoting starch catabolism and increasing soluble sugars to cope
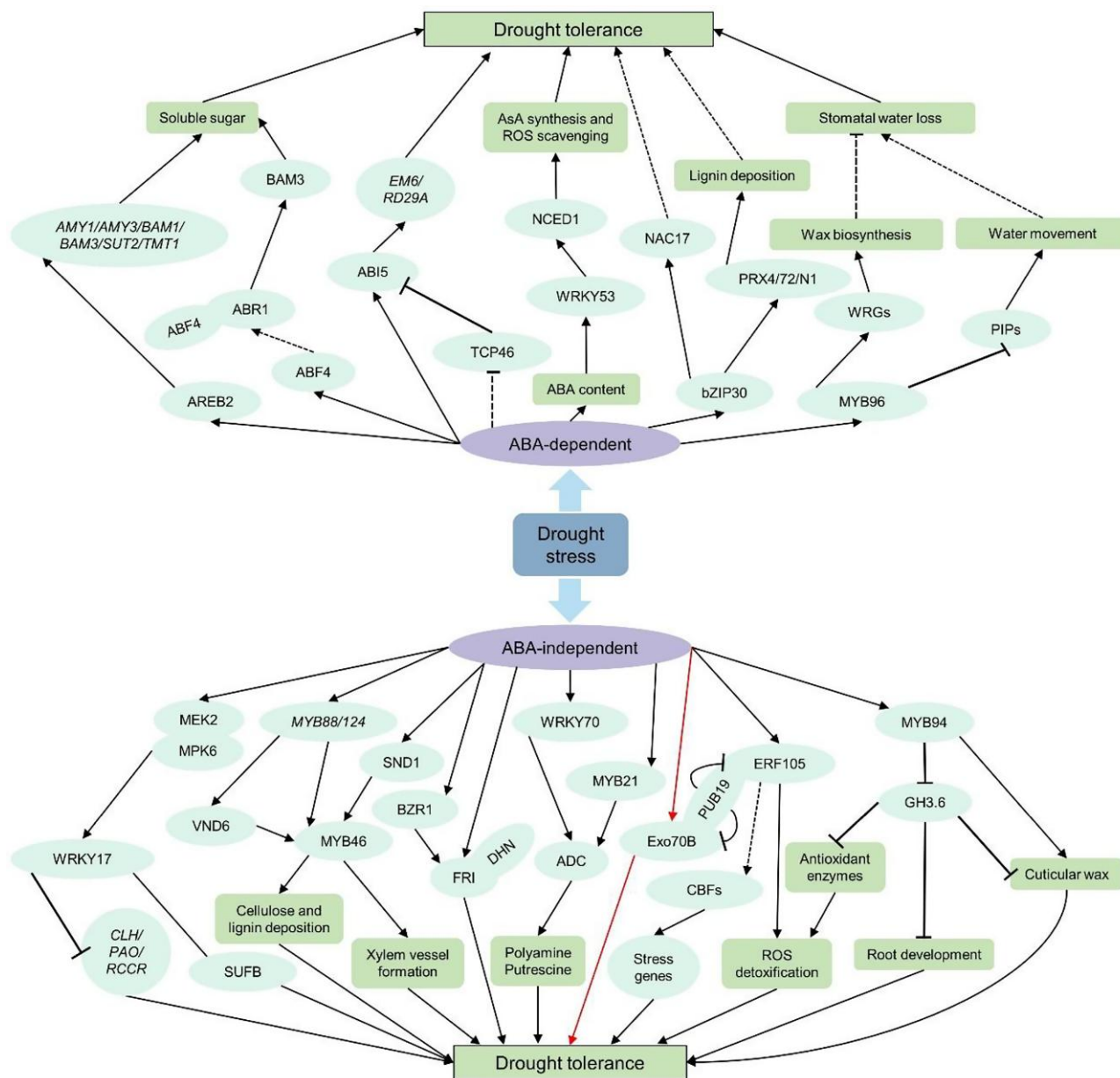
Figure 3. ABA-dependent and ABA-independent transcriptional regulatory pathways in fruit crops under drought stress. The solid arrows refer to direct effects, blocked arrows refer to inhibition, the dashed lines refer to indirect effects or unknown effects, and the red solid arrows refer to the regulation of drought stress via both ABA-dependent and ABA-independent pathways. AsA, ascorbic acid; ROS, reactive oxygen species; BAM, BARELY ANY MERISTEM; *EM6, EARLY METHIONINE-LABELED6; RD29A, RESPONSIVE TO DESICCATION29A*; NCED, 9-cis-epoxycarotenoid dioxygenase; AMY, amylase; SUT, Suc uptake transporter; TMT, tonoplast monosaccharide transporter; ABI, ABSCISIC ACID-INSENSITIVE; PRX, peroxidase; ABF, ABRE binding factor; ABR, ABA-responsive; AREB, ABA-responsive element binding protein; TCP, TEOSINTE BRANCHED 1/CYCLOIDEA/PCF; ABA, abscisic acid; WRG, wax-related genes; PIPs, plasma membrane intrinsic proteins; MEK, mitogen-activated protein kinase kinase; MPK, mitogen-activated protein kinase; SND, secondary wall-associated NAC domain protein; CLH, chlorophyllase; PAO, pheide a oxygenase; RCCR, red chlorophyll catabolite reductase; VND, VASCULAR-RELATED NAC DOMAIN; SUFB, a member of sulfur mobilization (SUF) system; BZR, brassinazole-resistant; FRI, FRIGIDA; DHN, dehydration protein; ADC, arginine decarboxylase; Exo70B, a subunit of exocyst; PUB, plant U-box E3 ubiquitin ligase; CBFs, C-REPEAT BINDING FACTORs; GH3.6, GRETCHEN HAGEN3.6.

with drought conditions. More interestingly, ABA-induced PtrABF4 also acts as a positive upstream regulator of *PtrABR1* to improve the transcript level of *PtrBAM3*. ABA signaling is triggered by water loss in *Citrus sinensis*, enhancing the expression levels of *CsMYB96*, which simultaneously binds to the promoters of *CsPIPs* (encoding plasma membrane intrinsic proteins) and three wax-related genes (*WRGs*) such as *ECERIFERUM1* (*CsCER1*) and *beta-ketoacyl-CoA synthases* (*CsKCS4* and *CsKCS12*). The inhibited *CsPIPs* expression blocks water movement and affects stomatal aperture, regulating

stomatal and nonstomatal water loss. In addition, the activated *WRG* expression increases wax biosynthesis, decreasing epidermal permeability and water loss ([Zhang et al. 2022b]). In pear (*Pyrus betulaefolia*), increased ABA contents induced by drought stress enhanced the expression of *PbrWRKY53*, which upregulates *PbrNCED1* (9-cis-type carotenoid dioxygenase, a key enzyme in the synthesis of ABA under drought) by binding to the W-box element in its promoter. AsA synthesis and ROS scavenging are promoted by the upregulated PbrWRKY53–PbrNCED1 module, alleviating drought-associated damage and improving drought resistance ([Liu et al. 2019]).

In ABA-independent regulation, MYB (v-myb avian myeloblastosis viral oncogene homolog), WRKY (so named because of the WRKYGQK heptapeptide at the N-terminal end), ERF (ethylene response factor), and BZR (brassinazole-resistant) regulons are critical in drought response and tolerance. In apple, water deficiency activates *MdMYB88* and *MdMYB124*, which bind to the promoters of *MdMYB46* and *VASCULAR-RELATED NAC-DOMAIN6* (*MdVND6*). The increased expression of *MdMYB46* causes cellulose and lignin deposition by activating the downstream genes related to cellulose and lignin biosynthesis to adapt to drought. Upregulated *MdMYB46* also improves hydraulic conductivity by regulating root xylem vessel formation, increasing drought tolerance ([Geng et al. 2018]). MdSND1 (secondary wall-associated NAC domain protein 1) has also been reported to regulate lignin biosynthesis by activating the transcription of *MdMYB46/83* and participating in the response to osmotic stress in apple plants ([Chen et al. 2020b]). [Jiang et al. (2022b)] identified a negative regulator of drought stress tolerance, GRETCHEN HAGEN3.6 (GH3.6), in apple plants. They found that MdGH3.6 negatively regulated root development, cuticular wax content, and antioxidant enzyme activity. However, MdMYB94 negatively regulated the promoters of *MdGH3.6* and positively regulated water-deficit tolerance in apple plants. In addition, drought stress activates MdWRKY17, which then binds to the promoters of *MdSUFB*, a gene encoding a member of sulfur mobilization system, and indirectly downregulates chlorophyll catabolic genes (chlorophyllase (*MdCLH*), pheide a oxygenase (*MdPAO*), and red chlorophyll catabolite reductase (*MdRCCR*) to maintain chlorophyll levels ([Shan et al. 2021]). Moreover, the phosphorylation of MdWRKY17 by the drought-activated MdMEK2–MdMPK6 cascade is important for fine-tuning the expression of *MdSUFB* to stabilize the chlorophyll content under moderate drought stress. In the grapevine *V. vinifera*, drought induces the expression of *VviERF105*, which interacts with VviPUB19 through its UND domain and is degraded by the E3 ubiquitin ligase VviPUB19. The upregulated *VviERF105* expression promotes the expression of *CBFs* (C-REPEAT BINDING FACTOR) and downstream resistance genes and inhibits ROS accumulation ([Wang et al. 2022a]). Since VviERF105-OE *Arabidopsis* showed lower sensitivity to ABA and higher resistance to mannitol and NaCl than the control group, it is possible that VviERF105 is not involved in plant abiotic stress via the ABA pathway ([Wang et al. 2022a]). [Wang et al. (2023)] also

demonstrated that VviPUB19 ubiquitinated and degraded VviExo70B (a subunit of exocyst). Under drought stress, the overexpression of *VviExo70B* may improve plant drought resistance by decreasing relative electrolyte leakages and increasing chlorophyll contents and survival rates in ABA-dependent and ABA-independent pathways. In citrus, drought stress induced the expression of CiBZR1, a member of the citrus BZR transcription factor family, which activated CiFRI (FRIGIDA, a key regulator of flowering time and drought tolerance) by binding to its promoter. Furthermore, the overexpression of CiFRI elevated the ability of ROS detoxification in transgenic lines under drought, and a dehydration protein (CiDHN) functioned as a CiFRI-stabilizing factor by interacting with CiFRI protein ([Xu et al. 2022b]). In a previous study, a dehydration treatment induced the expression of *FcWRKY70* in *Fortunella crassifolia*, and the overexpression of *FcWRKY70* in lemon (*C. limon*) improved the tolerance to drought stress by elevating putrescine levels via the regulation of the arginine decarboxylase gene ([Gong et al. 2015]). In *P. betulaefolia*, PbrMYB21 (a R2R3-type MYB), which acts as a positive regulator of drought tolerance, binds specifically to the *PbrADC* promoter. The elevated *PbrADC* expression levels cause accumulations of polyamine in *PbrMYB21* overexpressing tobacco (*Nicotiana tabacum*), improving drought tolerance ([Li et al. 2017b]).

miRNA responses

Plant miRNAs are 20 to 24 nucleotide noncoding RNAs that are vital in the responses to abiotic stresses ([Song et al. 2019]). Since miRNAs are relatively complex, we review mainly the recent progress in miRNA-related regulatory networks involved in the drought response in fruit crops ([Fig. 4]). In order to avoid repeating the content of several recent reviews on miRNAs or drought (not specifically for fruits), we do not discuss the classification and comparison of small RNAs ([Axtell 2013]), miRNA biogenesis ([Achkar et al. 2016]), the cell biology of miRNAs (the processes that miRNAs are involved in and the subcellular sites in which these processes take place) ([Yu et al. 2017]), the role of miRNAs in plant development ([Teotia and Tang 2015]; [Dong et al. 2022]), the effect of miRNAs on plant abiotic and biotic stress responses (excluding fruit crops) ([Sunkar et al. 2012]), and miRNA research progress made in *V. vinifera*, *Citrus spp*, *M. domestica*, and *P. persica* (the role of miRNAs in the drought response in fruit crops has not been reviewed, except for one paper on the role of miRNAs in peach crops) ([Solofoharivelo et al. 2014]).

The miRNA responses in grapevine have been reviewed in detail. [Rock (2013)] proposed that the evolution of trans-acting small interfering RNA gene 4 (TAS4) may be key to nutraceutical synthesis in grape development. Control of the expression of miRNAs ensures the beneficial effects of resveratrol, one of grape's polyphenols ([Lancon et al. 2012]). Recently, miRNAs regulating drought stress in apple plants have received increasing attention ([Fig. 4]). [Ma et al. (2014)] cloned 146 miRNA precursors from apple (11 of which were novel), identified the genomic location of miRNAs, and analyzed their expression levels in five different tissues.
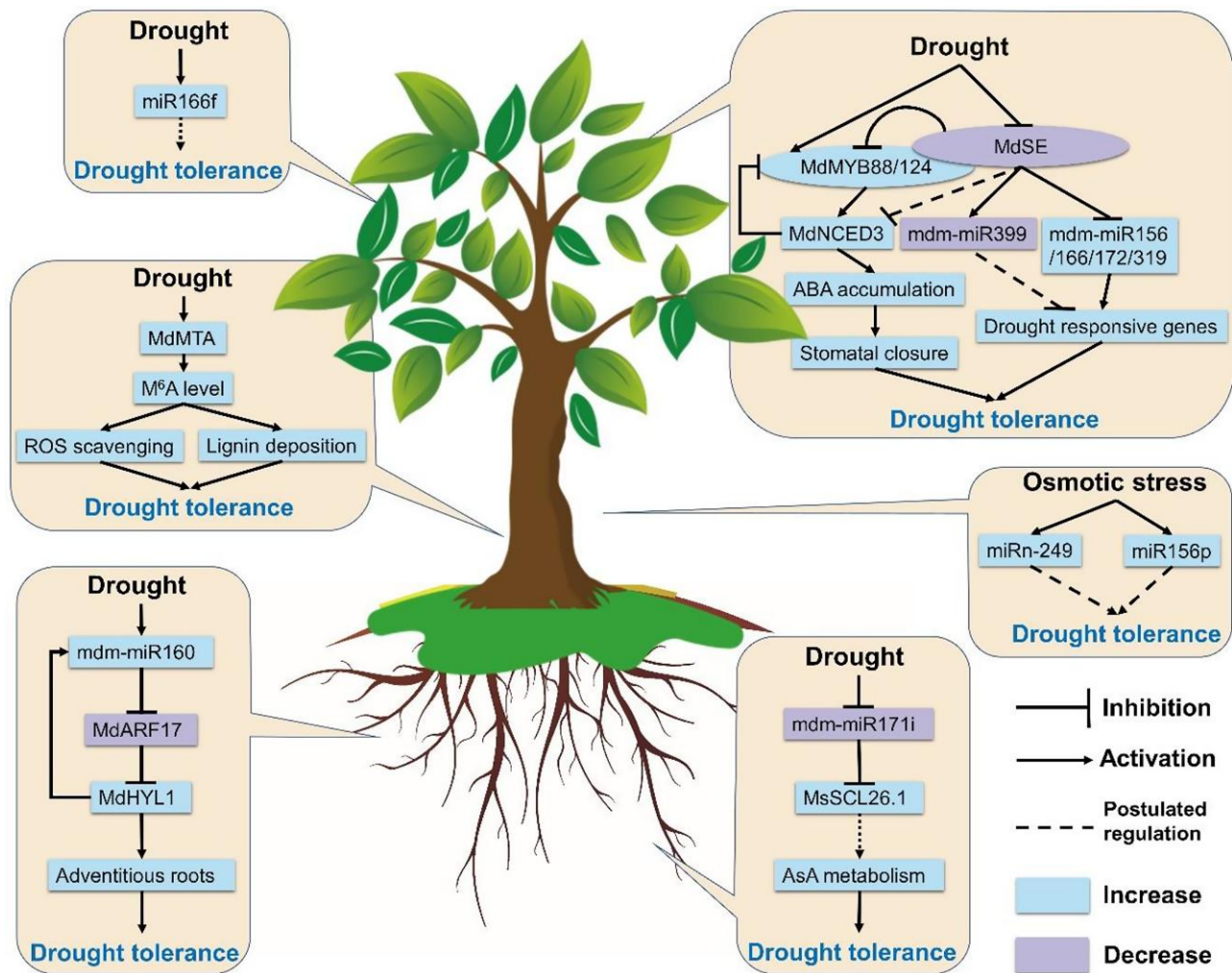
Figure 4. The regulatory roles of microRNAs (miRNAs) in fruit crops combating drought stress. The miR156p, miRn-249, mdm-miR160, mdm-miR171i, and miR166f respond to drought stimuli via regulating downstream genes. In addition, drought inhibits MdSE, which activates mdm-miR399 and inhibits mdm-miR156, mdm-miR166, mdm-miR172, and mdm-miR319, inducing the expression of drought-responsive genes. The m6A level of drought-responsive genes are increased by MdMTA to improve the drought tolerance. MTA, methylase; M^{6}A, N^6-methyladenosine; ROS, reactive oxygen species; ARF, AUXIN RESPONSE FACTOR; HYL, HYPONASTIC LEAVES; SE, SERRATE; NCED, 9-cis-epoxycarotenoid dioxygenase; ABA, abscisic acid; SCL, SCARECROW-LIKE PROTEINS; AsA, ascorbic acid.

Niu et al. (2019) identified 67 miRNAs that were differentially expressed under drought conditions in drought-tolerant apples compared with drought-sensitive apples. They verified that miR156p and miRn-249 played positive roles in osmotic stress tolerance. SERRATE is usually involved in miRNA biogenesis (Laubinger et al. 2008). Drought stress reduces the *MdSE* expression level, and MdSE interacts with and inhibits two positive regulators (MdMYB88 and its putative paralog MdMYB124) of the drought resistance of apple plants (*M. domestica*) (Li et al. 2020b; Xie et al. 2021). MdSE negatively regulates apple drought resistance by reducing the expression of mdm-miR156, mdm-miR166, mdm-miR172, and mdm-miR319 (positive regulators of osmotic stress), and increasing the expression of mdm-miR399 (a negative regulator of osmotic stress) (Li et al. 2020b). Interestingly, MdMYB88 directly binds to the promoter of the ABA

biosynthetic gene 9-cis-epoxycarotenoid dioxygenase 3 (*MdNCED3*) and promotes ABA accumulation, inhibiting *MdMYB88/124* expression under drought conditions (Xie et al. 2021). Coincidentally, MdSE is enriched in the MdNCED3 promoter in the same region where MdMYB88/124 binds and decreases MdNCED3 activity (Li et al. 2020b). MdSE consistently reduces ABA accumulation and stomatal aperture under drought stress (Li et al. 2020b). Plants modify their root system structure in response to drought conditions by increasing the length and number of adventitious roots for maximum water assimilation (Gilbert and Medina 2016). In *Arabidopsis*, the overexpression of miR160a and miR160c increased the number of adventitious roots, but the overexpression of the *AUXIN RESPONSE FACTOR17* (*ARF17*) reduced it (Gutierrez et al. 2009). In apple crops, Mdm-miR160 negatively targets MdARF17, which

interacts with HYPONASTIC LEAVES1 (MdHYL1) and negatively regulates the expression of MdHYL1, regulating the abundance of Mdm-miR160 (Shen et al. 2022). Mdm-miR160e OE, MdARF17 RNAi, and MdHYL1 OE transgenic apple plants have more root biomass and longer adventitious roots under drought conditions, suggesting that the drought tolerance of apple plants is influenced by the positive feedback loop of Mdm-miR160–MdARF17–MdHYL1 (Shen et al. 2022). Furthermore, drought inhibits the transcription level of mdm-miR171i, which negatively targets MsSCL26.1 (SCARECROW-LIKE PROTEINS26.1) in wild apple (*Malus sieversii*) plants, especially the roots (Wang et al. 2020). The antioxidant enzyme gene MONODEHYDROASCORBATE REDUCTASE (*MsMDHAR*) catalyzes the reduction of monodehydroascorbate into AsA, which might be upregulated by MsSCL26.1. The homeostasis of the AsA metabolism in plant cells is maintained to improve the drought tolerance of apple plants (Wang et al. 2020). When RNA transmits genetic information from DNA to proteins, various modifications of RNA transcripts occur. MTA (methylase, an ortholog of methyltransferase METTL3) is a methyltransferase and a component of N^6-methyladenosine (m^6A, the most common RNA modification) (Meyer et al. 2012). Drought stress induces the expression of *MdMTA* to increase the m^6A level of drought-responsive genes in apple plants (Hou et al. 2022). The mRNA stability and translation efficiency of genes involved in ROS scavenging and lignin deposition are promoted by the increased m^6A level, increasing the drought tolerance of apple plants (Hou et al. 2022).

In addition to apple plants, miR166f is a possible positive regulator of the drought tolerance of mulberry (*Morus multicaulis*) plants (Li et al. 2018b). Pagliarani et al. (2017) found that the concentration of drought-responsive miRNAs in different genotypes (a drought-tolerant grapevine rootstock, M4, *V. vinifera* × *Vitis berlandieri* and a commercial cultivar, Cabernet Sauvignon) was affected by reciprocal grafting, suggesting either miRNA transport between the scion and rootstock or signals triggering miRNA expression in the graft partner.

Strategies for overcoming drought stress

Breeding and biotechnology
Numerous strategies exist for plants to deal with drought (Fig. 5). A vital strategy is to plant drought-tolerant species that are more sustainable, economical, and ecologically friendly. Many fruit crop varieties with strong drought resistance have been identified (Wang et al. 2012; Liu et al. 2012a, 2012b; Wu et al. 2014b; Geng et al. 2019; Sousa et al. 2022). Although many drought-tolerant germplasms of fruit crops have been developed by breeding programs, reliable information on drought-tolerant or drought-sensitive accessions must be obtained by conducting experiments at different sites.

Autopolyploid fruit crops have received more attention than diploid progenitors due to their tolerance to abiotic stresses (Jiang et al. 2022a). Polyploid plants are characterized by small size, short internodes, and high stress tolerance. The development of polyploid rootstocks has become a popular strategy in recent years to improve the drought tolerance of fruit crops. Tetraploid lemon (*C. limonia* Osb.) (Vieira et al. 2016), tetraploid Rangpur lime citrus (Allario et al. 2013), and triploid citrus (Lourkisti et al. 2022) are more drought-tolerant than diploid types. Studies on the drought tolerance of citrus polyploids have demonstrated their superior drought tolerance. However, research on the drought resistance of other polyploid fruit crops must be strengthened.

Genome sequencing and resequencing provide data, molecular tools, and alternative approaches to plant breeding. In fruit crops, the presence of heterozygotes hinders the fidelity of genome assembly and results in numerous repetitive sequences. However, this problem can be circumvented by using doubled haploid lines in genome sequencing, resulting in high-quality genome combinations (Wu et al. 2014a). Recently, Sun et al. (2020) sequenced the heterozygous lines to reveal the diploid state of the genomes. The whole genome sequences of *Prunus humilis* (Wang et al. 2022c) and Illumina sequencing of pooled total RNA from drought-sensitive and drought-tolerant apple plants (Niu et al. 2019) have provided additional insights into drought adaption in fruit crops. However, whole genome sequencing and assembly is expensive and complex, whereas transcriptome analysis does not have these drawbacks. Qian et al. (2020) revealed the molecular regulatory mechanism of ABA-mediated drought tolerance in pomegranate (*Punica granatum* L.) via transcriptome analysis.

Numerous drought-responsive genes have been identified by various functional genomics approaches. Most of these genes were overexpressed or suppressed by utilizing transgenic technologies to improve plant drought tolerance (Hu and Xiong 2014). In recent years, precise genetic editing techniques, commonly referred to as genome editing techniques [such as zinc-finger nucleases, transcription activator-like effector nucleases, and the Clustered Regularly Interspaced Short Palindromic Repeats (CRISPR)/CRISPR-associated protein 9 (Cas9) system], have been developed. They do not have the biosafety problems associated with transgenic technology because precise genetic modifications are performed at specific sites (Hua et al. 2019). The CRISPR-Cas9 system is the most powerful and user-friendly genome editing tool due to its precision, efficiency, and simplicity. *VvEPFL9-1* (*Epidermal Patterning Factor Like9-1*) knockout through the CRISPR-Cas9 system reduces the stomatal density of grapevine, decreasing the use of irrigation water and increasing crop water-use efficiency (Clemens et al. 2022).

Horticultural management practices
Grafting fruit crops onto drought-tolerant rootstocks to improve water efficiency has been proposed as a fundamental strategy for coping with drought (Berdeja et al. 2015). Therefore, it is particularly important to understand the mechanism of rootstock–scion interaction and develop rootstocks that enhance the growth and productivity of offspring
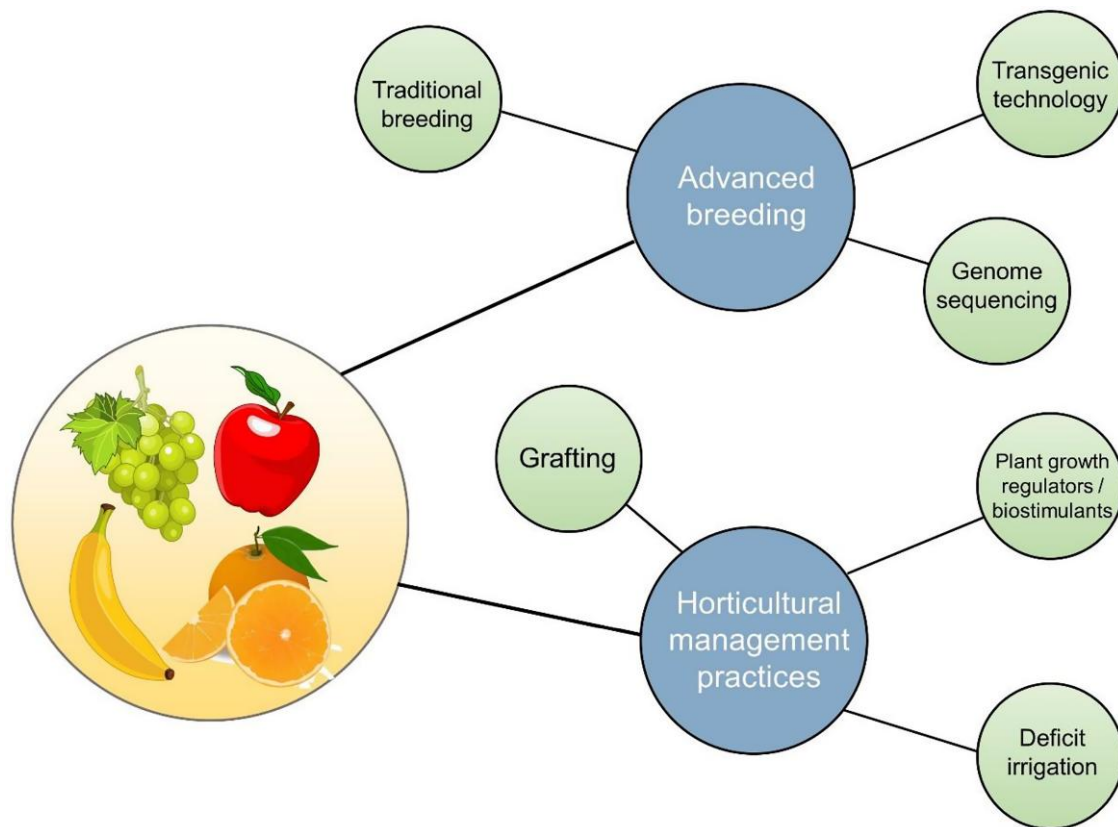
Figure 5. Strategies for overcoming drought in fruit crops. There are two strategies to reduce drought stress in fruit crops. One is advanced breeding, including traditional breeding, transgenic technology, and genome sequencing. Another is horticultural management practices, including grafting onto drought-tolerant rootstocks, using exogenous plant growth regulators and biostimulants, and water-deficit irrigation.

under drought conditions. Recently, the application of exogenous substances (plant growth regulators and biostimulants) to improve drought resistance and maintain the yield of fruit crops has become a research frontier (Basile et al. 2020). Arbuscular mycorrhizal fungi are widely used in fruit crops due to their capacity to improve plant mineral uptake. The enhanced drought tolerance may be closely related to the enhanced water absorption capacity of plants due to a change in the root structure (Wu et al. 2013). Moreover, the drought tolerance of apples is enhanced by the application of exogenous MT (Li et al. 2015, 2016; Liang et al. 2018b) and dopamine (Liang et al. 2018a; Gao et al. 2020). In addition, deficit irrigation has become increasingly popular to maintain crop production and conserve water in arid and semi-arid regions (El Jaouhari et al. 2018; Zuazo et al. 2021; Yang et al. 2022a). The main techniques are regulated deficit irrigation (targeted water reduction during certain phenological stages), partial root drying (partial root drying and alternating water stress), and sustained deficit irrigation (continuous water reduction throughout the phenological development of crops). The effects of the three deficit irrigation techniques on the growth and yield of fruit crops are different due to different experimental conditions (i.e. various cultivars, tree ages, climatic conditions, and soil types). The negative impacts of drought stress can be mitigated using drought-tolerant plant genotypes combined with adaptive agronomic practices (such as deficit irrigation, soil management, and plant density).

Conclusions and future directions

Drought entails many challenges and threats to fruit crops. Because fruit crops are mostly woody perennials (some are herbaceous perennials), research on their drought resistance is more complex than that of annual plants. Although drought slows vegetative growth and reduces the yield of fruit crops by affecting their root structure and photosynthesis, many studies have shown that moderate drought stress can improve fruit quality. The effect of drought on secondary metabolite production is paramount for fruit crops. Moderate drought stress promotes higher levels of healthy phytochemicals that may improve fruit quality. In addition, the activity of secondary metabolism may also help fruit crops cope with drought. However, the available data suggest that the basic mechanisms of drought adaptation in fruit crops can be better understood by analyzing well-known molecular mechanisms in model plants; much work remains to be done in this area (see Outstanding Questions).

In addition, many strategies have been proposed to improve the drought resistance of fruit crops. The application of exogenous substances (plant growth regulators and

biostimulants) is widely used to improve drought resistance and maintain the yield of fruit crops. Drought-tolerant varieties developed by traditional breeding methods and molecular-assisted breeding should be utilized in future agricultural production.

Many unknown factors must be elucidated in the future. The current understanding of the role of polyploidy in improving the drought resistance of fruit crops is based on experiments with very few species, primarily citrus fruits. These studies represent a small fraction of the diversity of fruit crops, and future studies should aim to increase the breadth of fruit crop species. Additionally, it is particularly important to breed rootstocks that improve the growth and productivity of offspring to resist drought. However, evaluating the quality of drought-tolerant rootstocks is complex. The identification of drought-tolerant rootstocks and the interaction between the rootstocks and scions of fruit crops require a substantial research effort (see Outstanding Questions). Furthermore, it is crucial to focus on strengthening the adaptability of different germplasm resources of fruit crops to drought stress to understand the effects of drought on fruit crops and the underlying mechanisms. The result will provide a scientific basis for identifying and selecting drought-tolerant genotypes and varieties of fruit crops.

OUTSTANDING QUESTIONS

- What is the mechanism of flower bud differentiation in response to drought in perennial woody fruit crops?
- What are the adaptation mechanisms of fruit crops to long-term moderate drought?
- Can polyploid rootstocks of fruit crops improve drought tolerance? What is the mechanism of rootstock–scion interaction?

Author Contributions

All authors participated in writing of the article. C.L. and F.M. revised the article critically for important intellectual content. Figures were developed by X.L. and T.G.

Funding

Conflict of interest statement. The authors declare no conflicts of interest.

Data availability

The data that support this review are openly available in a public repository.

References

Achkar NP, Cambiagno DA, Manavella PA. miRNA biogenesis: a dynamic pathway. Trends Plant Sci. 2016:**21**(12):1034–1044. https://doi.org/10.1016/j.tplants.2016.09.003

Allario T, Brumos J, Colmenero-Flores JM, Iglesias DJ, Pina JA, Navarro L, Talon M, Ollitrault P, Morillon R. Tetraploid Rangpur lime rootstock increases drought tolerance via enhanced constitutive root abscisic acid production. Plant Cell Environ. 2013:**36**(4): 856–868. https://doi.org/10.1111/pce.12021

Assmann SM, Jegla T. Guard cell sensory systems: recent insights on stomatal responses to light, abscisic acid, and CO_2. Curr Opin Plant Biol. 2016:**33**:157–167. https://doi.org/10.1016/j.pbi.2016.07.003

Axtell MJ. Classification and comparison of small RNAs from plants. Annu Rev Plant Biol. 2013:**64**(1):137–159. https://doi.org/10.1146/annurev-arplant-050312-120043

Balint G, Reynolds AG. Irrigation level and time of imposition impact vine physiology, yield components, fruit composition and wine quality of Ontario Chardonnay. Sci Hortic. 2017:**214**:252–272. https://doi.org/10.1016/j.scienta.2016.11.052

Bao Y, Song WM, Wang P, Yu X, Li B, Jiang C, Shiu SH, Zhang H, Bassham DC. COST1 regulates autophagy to control plant drought tolerance. Proc Natl Acad Sci USA. 2020:**117**(13):7482–7493. https://doi.org/10.1073/pnas.1918539117

Basile B, Rouphael Y, Colla G, Soppelsa S, Andreotti C. Appraisal of emerging crop management opportunities in fruit trees, grapevines and berry crops facilitated by the application of biostimulants. Sci Hortic. 2020:**267**:109330. https://doi.org/10.1016/j.scienta.2020.109330

Belin C, de Franco PO, Bourbousse C, Chaignepain S, Schmitter JM, Vavasseur A, Giraudat J, Barbier-Brygoo H, Thomine S. Identification of features regulating OST1 kinase activity and OST1 function in guard cells. Plant Physiol. 2006:**141**(4):1316–1327. https://doi.org/10.1104/pp.106.079327

Berdeja M, Nicolas P, Kappel C, Dai ZW, Hilbert G, Peccoux A, Lafontaine M, Ollat N, Gomès E, Delrot S. Water limitation and rootstock genotype interact to alter grape berry metabolism through transcriptome reprogramming. Hortic Res. 2015:**2**(1):15012. https://doi.org/10.1038/hortres.2015.12

Brandt B, Munemasa S, Wang C, Nguyen D, Yong TM, Yang PG, Poretsky E, Belknap TF, Waadt R, Aleman F, et al. Calcium specificity signaling mechanisms in abscisic acid signal transduction in *Arabidopsis* guard cells. Elife. 2015:**4**:e03599. https://doi.org/10.7554/eLife.03599

Brodribb TJ, McAdam SAM. Abscisic acid mediates a divergence in the drought response of two conifers. Plant Physiol. 2013:**162**(3): 1370–1377. https://doi.org/10.1104/pp.113.217877

Burger M. Escaping the drought: the OST1-VOZ1 module regulates early flowering in tomato. Plant Cell. 2022:**34**(5):1886–1887. https://doi.org/10.1093/plcell/koac042

Chen KQ, Guo YN, Song MR, Liu LF, Xue H, Dai HY, Zhang ZH. Dual role of *MdSND1* in the biosynthesis of lignin and in signal transduction in response to salt and osmotic stress in apple. Hortic Res. 2020b:**7**(1):204. https://doi.org/10.1038/s41438-020-00433-7

Chen K, Li GJ, Bressan RA, Song CP, Zhu JK, Zhao Y. Abscisic acid dynamics, signaling, and functions in plants. J Integr Plant Biol. 2020a:**62**(1):25–54. https://doi.org/10.1111/jipb.12899

Cheng LL, Zhou R, Reidel EJ, Sharkey TD, Dandekar AM. Antisense inhibition of sorbitol synthesis leads to up-regulation of starch synthesis without altering CO_2 assimilation in apple leaves. Planta. 2005:**220**(5):767–776. https://doi.org/10.1007/s00425-004-1384-5

Chung T, Phillips AR, Vierstra RD. ATG8 Lipidation and ATG8-mediated autophagy in Arabidopsis require ATG12 expressed from the differentially controlled ATG12A AND ATG12B loci. Plant J. 2010:**62**(3): 483–493. https://doi.org/10.1111/j.1365-313X.2010.04166.x

Clemens M, Faralli M, Lagreze J, Bontempo L, Piazza S, Varotto C, Malnoy M, Oechel W, Rizzoli A, Dalla Costa L. *VvEPFL9-1* knock-

out via CRISPR/Cas9 reduces stomatal density in grapevine. Front Plant Sci. 2022:**13**:878001. https://doi.org/10.3389/fpls.2022.878001

Cuellar T, Pascaud F, Verdeil JL, Torregrosa L, Adam-Blondon AF, Thibaud JB, Sentenac H, Gaillard I. A grapevine Shaker inward K$^+$ channel activated by the calcineurin B-like calcium sensor 1-protein kinase CIPK23 network is expressed in grape berries under drought stress conditions. Plant J. 2010:**61**(1):58–69. https://doi.org/10.1111/j.1365-313X.2009.04029.x

Danquah A, de Zelicourt A, Boudsocq M, Neubauer J, Frey NFD, Leonhardt N, Pateyron S, Gwinner F, Tamby JP, Ortiz-Masia D, et al. Identification and characterization of an ABA-activated MAP kinase cascade in *Arabidopsis thaliana*. Plant J. 2015:**82**(2):232–244. https://doi.org/10.1111/tpj.12808

Daszkowska-Golec A, Szarejko I. Open or close the gate-stomata action under the control of phytohormones in drought stress conditions. Front Plant Sci. 2013:**4**:138. https://doi.org/10.3389/fpls.2013.00138

de Zelicourt A, Colcombet J, Hirt H. The role of MAPK modules and ABA during abiotic stress signaling. Trends Plant Sci. 2016:**21**(8):677–685. https://doi.org/10.1016/j.tplants.2016.04.004

Dong QK, Hu BB, Zhang C. microRNAs and their roles in plant development. Front Plant Sci. 2022:**13**:824240. https://doi.org/10.3389/fpls.2022.824240

Drerup MM, Schlucking K, Hashimoto K, Manishankar P, Steinhorst L, Kuchitsu K, Kudla J. The calcineurin B-like calcium sensors CBL1 and CBL9 together with their interacting protein kinase CIPK26 regulate the *Arabidopsis* NADPH oxidase RBOHF. Mol Plant. 2013:**6**(2):559–569. https://doi.org/10.1093/mp/sst009

El Jaouhari N, Abouabdillah A, Bouabid R, Bourioug M, Aleya L, Chaoui M. Assessment of sustainable deficit irrigation in a Moroccan apple orchard as a climate change adaptation strategy. Sci Total Environ. 2018:**642**:574–581. https://doi.org/10.1016/j.scitotenv.2018.06.108

Faghih S, Zamani Z, Fatahi R, Omidi M. Influence of kaolin application on most important fruit and leaf characteristics of two apple cultivars under sustained deficit irrigation. Biol Res. 2021:**54**(1):1. https://doi.org/10.1186/s40659-020-00325-z

Fang YJ, Xiong LZ. General mechanisms of drought response and their application in drought resistance improvement in plants. Cell Mol Life Sci. 2015:**72**(4):673–689. https://doi.org/10.1007/s00018-014-1767-0

Gao TT, Wang YP, Liu Y, Ma MN, Li XP, Zhang DN, Ding K, Li C, Zou YJ, Ma FW. Overexpression of tyrosine decarboxylase (*MdTYDC*) enhances drought tolerance in *Malus domestica*. Sci Hortic. 2021:**289**:110425. https://doi.org/10.1016/j.scienta.2021.110425

Gao TT, Zhang ZJ, Liu XM, Wu Q, Chen Q, Liu QW, van Nocker S, Ma FW, Li C. Physiological and transcriptome analyses of the effects of exogenous dopamine on drought tolerance in apple. Plant Physiol Biochem. 2020:**148**:260–272. https://doi.org/10.1016/j.plaphy.2020.01.022

Geiger D, Scherzer S, Mumm P, Stange A, Marten I, Bauer H, Ache P, Matschi S, Liese A, Al-Rasheid KAS, et al. Activity of guard cell anion channel SLAC1 is controlled by drought-stress signaling kinase-phosphatase pair. Proc Natl Acad Sci USA. 2009:**106**(50):21425–21430. https://doi.org/10.1073/pnas.0912021106

Geng DL, Chen PX, Shen XX, Zhang Y, Li XW, Jiang LJ, Xie YP, Niu CD, Zhang J, Huang XH, et al. MdMYB88 and MdMYB124 enhance drought tolerance by modulating root vessels and cell walls in apple. Plant Physiol. 2018:**178**(3):1296–1309. https://doi.org/10.1104/pp.18.00502

Geng DL, Lu LY, Yan MJ, Shen XX, Jiang LJ, Li HY, Wang LP, Yan Y, Xu JD, Li CY, et al. Physiological and transcriptomic analyses of roots from *Malus sieversii* under drought stress. J Integr Agric. 2019:**18**(6):1280–1294. https://doi.org/10.1016/S2095-3119(19)62571-2

Gilbert ME, Medina V. Drought adaptation mechanisms should guide experimental design. Trends Plant Sci. 2016:**21**(8):639–647. https://doi.org/10.1016/j.tplants.2016.03.003

Gong Z, Xiong L, Shi H, Yang S, Herrera-Estrella LR, Xu G, Chao DY, Li J, Wang PY, Qin F, et al. Plant abiotic stress response and nutrient use efficiency. Sci China Life Sci. 2020:**63**(5):635–674. https://doi.org/10.1007/s11427-020-1683-x

Gong XQ, Zhang JY, Hu JB, Wang W, Wu H, Zhang QH, Liu JH. FcWRKY70, a WRKY protein of *Fortunella crassifolia*, functions in drought tolerance and modulates putrescine synthesis by regulating arginine decarboxylase gene. Plant Cell Environ. 2015:**38**(11):2248–2262. https://doi.org/10.1111/pce.12539

Gutierrez L, Bussell JD, Pacurar DI, Schwambach J, Pacurar M, Bellini C. Phenotypic plasticity of adventitious rooting in *Arabidopsis* is controlled by complex regulation of auxin response factor transcripts and microRNA abundance. Plant Cell. 2009:**21**(10):3119–3132. https://doi.org/10.1105/tpc.108.064758

Han JP, Koster P, Drerup MM, Scholz M, Li SZ, Edel KH, Hashimoto K, Kuchitsu K, Hippler M, Kudla J. Fine-tuning of RBOHF activity is achieved by differential phosphorylation and Ca^{2+} binding. New Phytol. 2019:**221**(4):1935–1949. https://doi.org/10.1111/nph.15543

Hou N, Li C, He J, Liu Y, Yu S, Malnoy M, Mobeen Tahir M, Xu L, Ma F, Guan Q. MdMTA-mediated m(6) A modification enhances drought tolerance by promoting mRNA stability and translation efficiency of genes involved in lignin deposition and oxidative stress. New Phytol. 2022:**234**(4):1294–1314. https://doi.org/10.1111/nph.18069

Hua DP, Wang C, He JN, Liao H, Duan Y, Zhu ZQ, Guo Y, Chen ZZ, Gong ZZ. A plasma membrane receptor kinase, GHR1, mediates abscisic acid- and hydrogen peroxide-regulated stomatal movement in Arabidopsis. Plant Cell. 2012:**24**(6):2546–2561. https://doi.org/10.1105/tpc.112.100107

Hu HH, Xiong LZ. Genetic engineering and breeding of drought-resistant crops. Annu Rev Plant Biol. 2014:**65**(1):715–741. https://doi.org/10.1146/annurev-arplant-050213-040000

Hua K, Zhang JS, Botella JR, Ma CL, Kong FJ, Liu BH, Zhu JK. Perspectives on the application of genome-editing technologies in crop breeding. Mol Plant. 2019:**12**(8):1047–1059. https://doi.org/10.1016/j.molp.2019.06.009

Jafari M, Shahsavar A. The effect of foliar application of melatonin on changes in secondary metabolite contents in two citrus species under drought stress conditions. Front Plant Sci. 2021:**12**:692735. https://doi.org/10.3389/fpls.2021.692735

Jafari M, Shahsavar AR, Talebi M, Hesami M. Exogenous melatonin protects lime plants from drought stress-induced damage by maintaining cell membrane structure, detoxifying ROS and regulating antioxidant systems. Horticulturae. 2022:**8**(3):257. https://doi.org/10.3390/horticulturae8030257

Jia X, Jia XM, Li TT, Wang Y, Sun X, Huo LQ, Wang P, Che RM, Gong XQ, Ma FW. MdATG5a induces drought tolerance by improving the antioxidant defenses and promoting starch degradation in apple. Plant Sci. 2021a:**312**:111052. https://doi.org/10.1016/j.plantsci.2021.111052

Jia X, Mao K, Wang P, Wang Y, Jia XM, Huo LQ, Sun X, Che RM, Gong XQ, Ma FW. Overexpression of *MdATG8i* improves water use efficiency in transgenic apple by modulating photosynthesis, osmotic balance, and autophagic activity under moderate water deficit. Hortic Res. 2021b:**8**(1):81. https://doi.org/10.1038/s41438-021-00521-2

Jiang JL, Yang N, Li L, Qin GW, Ren KX, Wang HT, Deng JR, Ding DK. Tetraploidy in *Citrus wilsonii* enhances drought tolerance via synergistic regulation of photosynthesis, phosphorylation, and hormonal changes. Front Plant Sci. 2022a:**13**:875011. https://doi.org/10.3389/fpls.2022.875011

Jiang LJ, Zhang DH, Liu C, Shen WY, He JQ, Yue QY, Niu CD, Yang F, Li XW, Shen XX, et al. MdGH3.6 is targeted by MdMYB94 and plays a negative role in apple water-deficit stress tolerance. Plant J. 2022b:**109**(5):1271–1289. https://doi.org/10.1111/tpj.15631

Joseph SV, Edirisinghe I, Burton-Freeman BM. Fruit polyphenols: a review of anti-inflammatory effects in humans. Crit Rev Food Sci Nutr. 2016:**56**(3):419–444. https://doi.org/10.1080/10408398.2013.767221

Kalladan R, Lasky JR, Chang TZ, Sharma S, Juenger TE, Verslues PAO. Natural variation identifies genes affecting drought-induced abscisic acid accumulation in *Arabidopsis thaliana*. Proc Natl Acad Sci USA. 2017:**114**(43):11536–11541. https://doi.org/10.1073/pnas.1705884114

Katsuta S, Masuda G, Bak H, Shinozawa A, Kamiyama Y, Umezawa T, Takezawa D, Yotsui I, Taji T, Sakata Y. Arabidopsis Raf-like kinases act as positive regulators of subclass III SnRK2 in osmostress signaling. Plant J. 2020:**103**(2):634–644. https://doi.org/10.1111/tpj.14756

Kulma A, Szopa J. Catecholamines are active compounds in plants. Plant Sci. 2007:**172**(3):433–440. https://doi.org/10.1016/j.plantsci.2006.10.013

Lamers J, van der Meer T, Testerink C. How plants sense and respond to stressful environments. Plant Physiol. 2020:**182**(4):1624–1635. https://doi.org/10.1104/pp.19.01464

Lancon A, Kaminski J, Tili E, Michaille JJ, Latruffe N. Control of microRNA expression as a new way for resveratrol to deliver its beneficial effects. J Agric Food Chem. 2012:**60**(36):8783–8789. https://doi.org/10.1021/jf301479v

Laubinger S, Sachsenberg T, Zeller G, Busch W, Lohmann JU, Rascht G, Weigel D. Dual roles of the nuclear cap-binding complex and SERRATE in pre-mRNA splicing and microRNA processing in *Arabidopsis thaliana*. Proc Natl Acad Sci USA. 2008:**105**(25):8795–8800. https://doi.org/10.1073/pnas.0802493105

Li XW, Chen PX, Xie YP, Yan Y, Wang L, Dang H, Zhang J, Xu L, Ma FW, Guan QM. Apple SERRATE negatively mediates drought resistance by regulating MdMYB88 and MdMYB124 and microRNA biogenesis. Hortic Res. 2020b:**7**(1):98. https://doi.org/10.1038/s41438-020-0320-6

Li RX, Fan T, Wang TC, Dominic K, Hu F, Liu L, Zhang L, Fang RJ, Pan G, Li L, et al. Characterization and functional analysis of miR166f in drought stress tolerance in mulberry (*Morus multicaulis*). Mol Breed. 2018b:**38**(11):132. https://doi.org/10.1007/s11032-018-0886-y

Li JX, Hou XJ, Zhu J, Zhou JJ, Huang HB, Yue JQ, Gao JY, Du YX, Hu CX, Hu CG, et al. Identification of genes associated with lemon floral transition and flower development during floral inductive water deficits: a hypothetical model. Front Plant Sci. 2017a:**8**:01013. https://doi.org/10.3389/fpls.2017.01013

Li MJ, Li PM, Ma FW, Dandekar AM, Cheng LL. Sugar metabolism and accumulation in the fruit of transgenic apple trees with decreased sorbitol synthesis. Hortic Res. 2018a:**5**(1):60. https://doi.org/10.1038/s41438-018-0064-8

Li C, Liang BW, Chang C, Wei ZW, Zhou SS, Ma FW. Exogenous melatonin improved potassium content in *Malus* under different stress conditions. J Pineal Res. 2016:**61**(2):218–229. https://doi.org/10.1111/jpi.12342

Li CL, Meng D, Pineros MA, Mao YX, Dandekar AM, Cheng LL. A sugar transporter takes up both hexose and sucrose for sorbitol-modulated in vitro pollen tube growth in apple. Plant Cell. 2020a:**32**(2):449–469. https://doi.org/10.1105/tpc.19.00638

Li C, Tan DX, Liang D, Chang C, Jia DF, Ma FW. Melatonin mediates the regulation of ABA metabolism, free-radical scavenging, and stomatal behaviour in two *Malus* species under drought stress. J Exp Bot. 2015:**66**(3):669–680. https://doi.org/10.1093/jxb/eru476

Li KQ, Xing CH, Yao ZH, Huang XS. *PbrMYB21*, a novel MYB protein of *Pyrus betulaefolia*, functions in drought tolerance and modulates polyamine levels by regulating arginine decarboxylase gene. Plant Biotechnol J. 2017b:**15**(9):1186–1203. https://doi.org/10.1111/pbi.12708

Liang BW, Gao TT, Zhao Q, Ma CQ, Chen Q, Wei ZW, Li CY, Li C, Ma FW. Effects of exogenous dopamine on the uptake, transport, and resorption of apple ionome under moderate drought. Front Plant Sci. 2018a:**9**:755. https://doi.org/10.3389/fpls.2018.00755

Liang BW, Ma CQ, Zhang ZJ, Wei ZW, Gao TT, Zhao Q, Ma FW, Li C. Long-term exogenous application of melatonin improves nutrient uptake fluxes in apple plants under moderate drought stress. Environ Exp Bot. 2018b:**155**:650–661. https://doi.org/10.1016/j.envexpbot.2018.08.016

Liang D, Ni ZY, Xia H, Xie Y, Lv XL, Wang J, Lin LJ, Deng QX, Luo X. Exogenous melatonin promotes biomass accumulation and photosynthesis of kiwifruit seedlings under drought stress. Sci Hortic. 2019:**246**:34–43. https://doi.org/10.1016/j.scienta.2018.10.058

Liao CY, Bassham DC. Combating stress: the interplay between hormone signaling and autophagy in plants. J Exp Bot. 2020:**71**(5):1723–1733. https://doi.org/10.1093/jxb/erz515

Liu YJ, An JP, Gao N, Wang X, Chen XX, Wang XF, Zhang S, You CX. MdTCP46 interacts with MdABI5 to negatively regulate ABA signalling and drought response in apple. Plant Cell Environ. 2022:**45**(11):3233–3248. https://doi.org/10.1111/pce.14429

Liu BH, Cheng L, Ma FW, Liang D, Zou YJ. Influence of rootstock on drought response in young 'Gale Gala' apple (*Malus domestica* Borkh.) trees. J Sci Food Agric. 2012a:**92**(12):2421–2427. https://doi.org/10.1002/jsfa.5647

Liu BH, Cheng L, Ma FW, Zou YJ, Liang D. Growth, biomass allocation, and water use efficiency of 31 apple cultivars grown under two water regimes. Agrofor Syst. 2012b:**84**(2):117–129. https://doi.org/10.1007/s10457-011-9427-y

Liu YH, Offler C, Ruan YL. Regulation of fruit and seed response to heat and drought by sugars as nutrients and signals. Front Plant Sci. 2013:**4**:00282. https://doi.org/10.3389/fpls.2013.00282

Liu X, Wang JW, Sun LF. Structure of the hyperosmolality-gated calcium-permeable channel OSCA1.2. Nat Commun. 2018:**9**(1):5060. https://doi.org/10.1038/s41467-018-07564-5

Liu Y, Yang TY, Lin ZK, Gu BJ, Xing CH, Zhao LY, Dong HZ, Gao JZ, Xie ZH, Zhang SL, et al. A WRKY transcription factor PbrWRKY53 from *Pyrus betulaefolia* is involved in drought tolerance and AsA accumulation. Plant Biotechnol J. 2019:**17**(9):1770–1787. https://doi.org/10.1111/pbi.13099

Lobet G, Draye X. Novel scanning procedure enabling the vectorization of entire rhizotron-grown root systems. Plant Methods. 2013:**9**(1):1. https://doi.org/10.1186/1746-4811-9-1

Lo Bianco R, Rieger M, Sung SJS. Effect of drought on sorbitol and sucrose metabolism in sinks and sources of peach. Physiol Plant. 2000:**108**(1):71–78. https://doi.org/10.1034/j.1399-3054.2000.108001071.x

Lobos TE, Retamales JB, Ortega-Farias S, Hanson EJ, Lopez-Olivari R, Mora ML. Regulated deficit irrigation effects on physiological parameters, yield, fruit quality and antioxidants of *Vaccinium corymbosum* plants cv. Brigitta. Irrig Sci. 2018:**36**(1):49–60. https://doi.org/10.1007/s00271-017-0564-6

Lourkisti R, Froelicher Y, Morillon R, Berti L, Santini J. Enhanced photosynthetic capacity, osmotic adjustment and antioxidant defenses contribute to improve tolerance to moderate water deficit and recovery of triploid citrus genotypes. Antioxidants. 2022:**11**(3):562. https://doi.org/10.3390/antiox11030562

Lynch JP. Root phenotypes for improved nutrient capture: an underexploited opportunity for global agriculture. New Phytol. 2019:**223**(2):548–564. https://doi.org/10.1111/nph.15738

Ma C, Lu Y, Bai SL, Zhang WN, Duan XW, Meng D, Wang ZG, Wang A, Zhou ZS, Li TZ. Cloning and characterization of miRNAs and their targets, including a novel miRNA-targeted NBS–LRR protein class gene in apple (Golden Delicoius). Mol Plant. 2014:**7**(1):218–230. https://doi.org/10.1093/mp/sst101

Ma QJ, Sun MH, Lu J, Liu YJ, Hu DG, Hao YJ. Transcription factor AREB2 is involved in soluble sugar accumulation by activating sugar transporter and amylase genes. Plant Physiol. 2017:**174**(4):2348–2362. https://doi.org/10.1104/pp.17.00502

Ma Y, Szostkiewicz I, Korte A, Moes D, Yang Y, Christmann A, Grill E. Regulators of PP2C phosphatase activity function as abscisic acid sensors. Science. 2009:**324**(5930):1064–1068. https://doi.org/10.1126/science.1172408

Maierhofer T, Diekmann M, Offenborn JN, Lind C, Bauer H, Hashimoto K, Al-Rasheid KAS, Luan S, Kudla J, Geiger D, et al.

Site-and kinase-specific phosphorylation-mediated activation of SLAC1, a guard cell anion channel stimulated by abscisic acid. Sci Signal. 2014:**7**(342):ra86. https://doi.org/10.1126/scisignal.2005703

Maity K, Heumann JM, McGrath AP, Kopcho NJ, Hsu PK, Lee CW, Mapes JH, Garza D, Krishnan S, Morgan GP, et al. Cryo-EM structure of OSCA1.2 from *Oryza sativa* elucidates the mechanical basis of potential membrane hyperosmolality gating. Proc Natl Acad Sci USA. 2019:**116**(28):14309–14318. https://doi.org/10.1073/pnas.1900774116

McMullin S, Njogu K, Wekesa B, Gachuiri A, Ngethe E, Stadlmayr B, Jamnadass R, Kehlenbeck K. Developing fruit tree portfolios that link agriculture more effectively with nutrition and health: a new approach for providing year-round micronutrients to smallholder farmers. Food Secur. 2019:**11**(6):1355–1372. https://doi.org/10.1007/s12571-019-00970-7

Meng D, He MY, Bai Y, Xu HX, Dandekar AM, Fei ZJ, Cheng LL. Decreased sorbitol synthesis leads to abnormal stamen development and reduced pollen tube growth via an MYB transcription factor, MdMYB39L, in apple (*Malus domestica*). New Phytol. 2018a:**217**(2):641–656. https://doi.org/10.1111/nph.14824

Meng D, Li CL, Park HJ, Gonzalez J, Wang JY, Dandekar AM, Turgeon BG, Cheng LL. Sorbitol modulates resistance to *Alternaria alternata* by regulating the expression of an *NLR* resistance gene in apple. Plant Cell. 2018b:**30**(7):1562–1581. https://doi.org/10.1105/tpc.18.00231

Meng JF, Xu TF, Wang ZZ, Fang YL, Xi ZM, Zhang ZW. The ameliorative effects of exogenous melatonin on grape cuttings under water-deficient stress: antioxidant metabolites, leaf anatomy, and chloroplast morphology. J Pineal Res. 2014:**57**(2):200–212. https://doi.org/10.1111/jpi.12159

Meyer KD, Saletore Y, Zumbo P, Elemento O, Mason CE, Jaffrey SR. Comprehensive analysis of mRNA methylation reveals enrichment in 3′ UTRs and near stop codons. Cell. 2012:**149**(7):1635–1646. https://doi.org/10.1016/j.cell.2012.05.003

Miller G, Suzuki N, Ciftci-Yilmaz S, Mittler R. Reactive oxygen species homeostasis and signalling during drought and salinity stresses. Plant Cell Environ. 2010:**33**(4):453–467. https://doi.org/10.1111/j.1365-3040.2009.02041.x

Miras-Avalos JM, Alcobendas R, Alarcon JJ, Valsesia P, Genard M, Nicolas E. Assessment of the water stress effects on peach fruit quality and size using a fruit tree model, QualiTree. Agric Water Manag. 2013:**130**:178–178. https://doi.org/10.1016/j.agwat.2013.08.021

Miura K, Okamoto H, Okuma E, Shiba H, Kamada H, Hasegawa PM, Murata Y. SIZ1 deficiency causes reduced stomatal aperture and enhanced drought tolerance via controlling salicylic acid-induced accumulation of reactive oxygen species in *Arabidopsis*. Plant J. 2013:**73**(1):91–104. https://doi.org/10.1111/tpj.12014

Morris EC, Griffiths M, Golebiowska A, Mairhofer S, Burr-Hersey J, Goh T, von Wangenheim D, Atkinson B, Sturrock CJ, Lynch JP, et al. Shaping 3D root system architecture. Curr Biol. 2017:**27**(17):919–930. https://doi.org/10.1016/j.cub.2017.06.043

Negm FB, Loescher WH. Characterization and partial purification of aldose-6-phosphate reductase (alditol-6-phosphate: NADP 1-oxidoreductase) from apple leaves. Plant Physiol. 1981:**67**(1):139–142. https://doi.org/10.1104/pp.67.1.139

Niu CD, Li HY, Jiang LJ, Yan MJ, Li CY, Geng DL, Xie YP, Yan Y, Shen XX, Chen PX, et al. Genome-wide identification of drought-responsive microRNAs in two sets of *Malus* from interspecific hybrid progenies. Hortic Res. 2019:**6**(1):75. https://doi.org/10.1038/s41438-019-0157-z

Nolan TM, Vukašinović N, Liu D, Russinova E, Yin Y. Brassinosteroids: multidimensional regulators of plant growth, development, and stress responses. Plant Cell. 2019:**32**(2):295–318. https://doi.org/10.1105/tpc.19.00335

Pagliarani C, Vitali M, Ferrero M, Vitulo N, Incarbone M, Lovisolo C, Valle G, Schubert A. The accumulation of miRNAs differentially modulated by drought stress is affected by grafting in grapevine. Plant Physiol. 2017:**173**(4):2180–2195. https://doi.org/10.1104/pp.16.01119

Park S, Byeon Y, Back K. Functional analyses of three *ASMT* gene family members in rice plants. J Pineal Res. 2013:**55**(4):409–415. https://doi.org/10.1111/jpi.12088

Park SY, Fung P, Nishimura N, Jensen DR, Fujii H, Zhao Y, Lumba S, Santiago J, Rodrigues A, Chow TFF, et al. Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. Science. 2009:**324**(5930):1068–1071. https://doi.org/10.1126/science.1173041

Qian JJ, Zhang XP, Yan Y, Wang N, Ge WQ, Zhou Q, Yang YC. Unravelling the molecular mechanisms of abscisic acid-mediated drought-stress alleviation in pomegranate (*Punica granatum* L.). Plant Physiol Biochem. 2020:**157**:211–218. https://doi.org/10.1016/j.plaphy.2020.10.020

Rachappanavar V, Padiyal A, Sharma JK, Gupta SK. Plant hormone-mediated stress regulation responses in fruit crops—a review. Sci Hortic. 2022:**304**:11130200000000000. https://doi.org/10.1016/j.scienta.2022.111302

Rao S, Tian Y, Zhang C, Qin Y, Liu M, Niu S, Li Y, Chen J. The JASMONATE ZIM-domain-OPEN STOMATA1 cascade integrates jasmonic acid and abscisic acid signaling to regulate drought tolerance by mediating stomatal closure in poplar. J Exp Bot. 2023:**74**(1):443–457. https://doi.org/10.1093/jxb/erac418

Rock CD. *Trans-acting small interfering RNA4*: key to nutraceutical synthesis in grape development? Trends Plant Sci. 2013:**18**(11):601–610. https://doi.org/10.1016/j.tplants.2013.07.006

Rowe JH, Topping JF, Liu J, Lindsey K. Abscisic acid regulates root growth under osmotic stress conditions via an interacting hormonal network with cytokinin, ethylene and auxin. New Phytol. 2016:**211**(1):225–239. https://doi.org/10.1111/nph.13882

Sabbadini S, Capocasa F, Battino M, Mazzoni L, Mezzetti B. Improved nutritional quality in fruit tree species through traditional and biotechnological approaches. Trends Food Sci Technol. 2021:**117**:125–138. https://doi.org/10.1016/j.tifs.2021.01.083

Shan DQ, Wang CY, Song HD, Bai YX, Zhang HX, Hu ZH, Wang L, Shi K, Zheng XD, Yan TC, et al. The MdMEK2-MdMPK6-MdWRKY17 pathway stabilizes chlorophyll levels by directly regulating MdSUFB in apple under drought stress. Plant J. 2021:**108**(3):814–828. https://doi.org/10.1111/tpj.15480

Sharma A, Wang JF, Xu DB, Tao SC, Chong SL, Yan DL, Li Z, Yuan HW, Zheng BS. Melatonin regulates the functional components of photosynthesis, antioxidant system, gene expression, and metabolic pathways to induce drought resistance in grafted *Carya cathayensis* plants. Sci Total Environ. 2020:**713**:136675. https://doi.org/10.1016/j.scitotenv.2020.136675

Shen XX, He JQ, Ping YK, Guo JX, Hou N, Cao FG, Li XW, Geng DL, Wang SC, Chen PX, et al. The positive feedback regulatory loop of miR160-Auxin Response Factor 17-HYPONASTIC LEAVES 1 mediates drought tolerance in apple trees. Plant Physiol. 2022:**188**(3):1686–1708. https://doi.org/10.1093/plphys/kiab565

Silva SF, Miranda MT, Cunha CP, Domingues AP, Aricetti JA, Caldana C, Machado EC, Ribeiro RV. Metabolic profiling of drought tolerance: revealing how citrus rootstocks modulate plant metabolism under varying water availability. Environ Exp Bot. 2023:**206**:105169. https://doi.org/10.1016/j.envexpbot.2022.105169

Solofoharivelo MC, van der Walt AP, Stephan D, Burger JT, Murray SL. MicroRNAs in fruit trees: discovery, diversity and future research directions. Plant Biol. 2014:**16**(5):856–865. https://doi.org/10.1111/plb.12153

Song SJ, Feng QN, Li CL, Li E, Liu Q, Kang H, Zhang W, Zhang Y, Li S. A tonoplast-associated calcium-signaling module dampens ABA signaling during stomatal movement. Plant Physiol. 2018:**177**(4):1666–1678. https://doi.org/10.1104/pp.18.00377

Song XW, Li Y, Cao XF, Qi YJ. MicroRNAs and their regulatory roles in plant-environment interactions. Annu Rev Plant Biol. 2019:**70**(1):489–525. https://doi.org/10.1146/annurev-arplant-050718-100334

Sousa ARdO, Silva EMdA, Filho MAC, Costa MGC, Filho WdSS, Micheli F, Maserti B, Gesteira AdS. Metabolic responses to drought

stress and rehydration in leaves and roots of three citrus scion/rootstock combinations. Sci Hortic. 2022:**292**:110490. https://doi.org/10.1016/j.scienta.2021.110490

Sun XP, Jiao C, Schwaninger H, Chao CT, Ma YM, Duan NB, Khan A, Ban S, Xu KN, Cheng LL, et al. Phased diploid genome assemblies and pan-genomes provide insights into the genetic history of apple domestication. Nat Genet. 2020:**52**(12):1423–1432. https://doi.org/10.1038/s41588-020-00723-9

Sun X, Wang P, Jia X, Huo LQ, Che RM, Ma FW. Improvement of drought tolerance by overexpressing *MdATG18a* is mediated by modified antioxidant system and activated autophagy in transgenic apple. Plant Biotechnol J. 2018:**16**(2):545–557. https://doi.org/10.1111/pbi.12794

Sun TT, Zhang JK, Zhang Q, Li XL, Li MJ, Yang YZ, Zhou J, Wei QP, Zhou BB. Exogenous application of acetic acid enhances drought tolerance by influencing the MAPK signaling pathway induced by ABA and JA in apple plants. Tree Physiol. 2022:**42**(9):1827–1840. https://doi.org/10.1093/treephys/tpac034

Sunkar R, Li YF, Jagadeeswaran G. Functions of microRNAs in plant stress responses. Trends Plant Sci. 2012:**17**(4):196–203. https://doi.org/10.1016/j.tplants.2012.01.010

Świędrych A, Lorenc-Kukula K, Skirycz A, Szopa J. The catecholamine biosynthesis route in potato is affected by stress. Plant Physiol Biochem. 2004:**42**(7–8):593–600. https://doi.org/10.1016/j.plaphy.2004.07.002

Takahashi F, Suzuki T, Osakabe Y, Betsuyaku S, Kondo Y, Dohmae N, Fukuda H, Yamaguchi-Shinozaki K, Shinozaki K. A small peptide modulates stomatal control via abscisic acid in long-distance signalling. Nature. 2018:**556**(7700):235–238. https://doi.org/10.1038/s41586-018-0009-2

Tang J, Bassham DC. Autophagy during drought: function, regulation, and potential application. Plant J. 2022:**109**(2):390–401. https://doi.org/10.1111/tpj.15481

Teotia S, Tang G. To bloom or not to bloom: role of microRNAs in plant flowering. Mol Plant. 2015:**8**(3):359–377. https://doi.org/10.1016/j.molp.2014.12.018

Tu MX, Wang XH, Yin WC, Wang Y, Li YJ, Zhang GF, Li Z, Song JY, Wang XP. Grapevine *VlbZIP30* improves drought resistance by directly activating *VvNAC17* and promoting lignin biosynthesis through the regulation of three peroxidase genes. Hortic Res. 2020:**7**(1):150. https://doi.org/10.1038/s41438-020-00372-3

Tu MX, Wang XH, Zhu YX, Wang DJ, Zhang XC, Cui Y, Li YJ, Gao M, Li Z, Wang YJ, et al. VlbZIP30 of grapevine functions in dehydration tolerance via the abscisic acid core signaling pathway. Hortic Res. 2018:**5**(1):49. https://doi.org/10.1038/s41438-018-0054-x

Vieira DDSS, Emiliani G, Michelozzi M, Centritto M, Luro F, Morillon R, Loreto F, Gesteira A, Maserti B. Polyploidization alters constitutive content of volatile organic compounds (VOC) and improves membrane stability under water deficit in Volkamer lemon (*Citrus limonia* Osb.) leaves. Environ Exp Bot. 2016:**126**:1–9. https://doi.org/10.1016/j.envexpbot.2016.02.010

Wang D, Chen QY, Chen WW, Guo QG, Xia Y, Wang SM, Jing DL, Liang GL. Physiological and transcription analyses reveal the regulatory mechanism of melatonin in inducing drought resistance in loquat (*Eriobotrya japonica* Lindl.) seedlings. Environ Exp Bot. 2021a:**181**:104291. https://doi.org/10.1016/j.envexpbot.2020.104291

Wang YP, Chen Q, Zheng JZ, Zhang ZJ, Gao TT, Li C, Ma FW. Overexpression of the tyrosine decarboxylase gene *MdTyDC* in apple enhances long-term moderate drought tolerance and WUE. Plant Sci. 2021b:**313**:111064. https://doi.org/10.1016/j.plantsci.2021.111064

Wang YT, Feng C, Zhai ZF, Peng X, Wang YY, Sun YT, Li J, Shen XS, Xiao YQ, Zhu SJ, et al. The apple microR171i-SCARECROW-LIKE PROTEINS26.1 module enhances drought stress tolerance by integrating ascorbic acid metabolism. Plant Physiol. 2020:**184**(1):194–211. https://doi.org/10.1104/pp.20.00476

Wang L, Feng C, Zheng X, Guo Y, Zhou F, Shan D, Liu X, Kong J. Plant mitochondria synthesize melatonin and enhance the tolerance of plants to drought stress. J Pineal Res. 2017a:**63**(3):e12429. https://doi.org/10.1111/jpi.12429

Wang XX, Gao YA, Wang QJ, Chen M, Ye XL, Li DM, Chen XD, Li L, Gao DS. 24-Epibrassinolide-alleviated drought stress damage influences antioxidant enzymes and autophagy changes in peach (*Prunus persicae* L.) leaves. Plant Physiol Biochem. 2019:**135**:30–40. https://doi.org/10.1016/j.plaphy.2018.11.026

Wang SC, Liang D, Li C, Hao YL, Ma FW, Shu HR. Influence of drought stress on the cellular ultrastructure and antioxidant system in leaves of drought-tolerant and drought-sensitive apple rootstocks. Plant Physiol Biochem. 2012:**51**:81–89. https://doi.org/10.1016/j.plaphy.2011.10.014

Wang P, Qi SJ, Wang XH, Dou LR, Jia MA, Mao TL, Guo YS, Wang XF. The OPEN STOMATA1-SPIRAL1 module regulates microtubule stability during abscisic acid-induced stomatal closure in *Arabidopsis*. Plant Cell. 2022b:**35**(1):260–278. https://doi.org/10.1093/plcell/koac1307

Wang P, Sun X, Jia X, Ma FW. Apple autophagy-related protein MdATG3s afford tolerance to multiple abiotic stresses. Plant Sci. 2017b:**256**:53–64. https://doi.org/10.1016/j.plantsci.2016.12.003

Wang P, Sun X, Li C, Wei ZW, Liang D, Ma FW. Long-term exogenous application of melatonin delays drought-induced leaf senescence in apple. J Pineal Res. 2013b:**54**(3):292–302. https://doi.org/10.1111/jpi.12017

Wang P, Sun X, Yue ZY, Liang D, Wang N, Ma FW. Isolation and characterization of *MdATG18a*, a WD40-repeat AuTophaGy-related gene responsive to leaf senescence and abiotic stress in *Malus*. Sci Hortic. 2014:**165**:51–61. https://doi.org/10.1016/j.scienta.2013.10.038

Wang Y, Xie J, Zhang HN, Li WD, Wang ZJ, Li HY, Tong Q, Qiao GX, Liu YJ, Tian Y, et al. The genome of *Prunus humilis* provides new insights to drought adaption and population diversity. DNA Res. 2022c:**29**(4):dsac021. https://doi.org/10.1093/dnares/dsac021

Wang MY, Yuan FF, Hao HM, Zhang YF, Zhao HX, Guo AG, Hu JJ, Zhou XN, Xie CG. BolOST1, an ortholog of Open Stomata 1 with alternative splicing products in *Brassica oleracea*, positively modulates drought responses in plants. Biochem Biophys Res Commun. 2013a:**442**(3–4):214–220. https://doi.org/10.1016/j.bbrc.2013.11.032

Wang L, Zhang X, Qu ZY, Guo WC, van Nocker S, Zhang CH. Grapevine *VviERF105* promotes tolerance to abiotic stress and is degraded by the E3 ubiquitin ligase VviPUB19. Environ Exp Bot. 2022a:**201**(102–113):105001. https://doi.org/10.1016/j.envexpbot.2022.105001

Wang L, Zhang X, Tang YJ, Zhao T, Huang CB, Li Y, Zhang CH. Exocyst subunit VviExo70B is degraded by ubiquitin ligase VviPUB19 and they regulate drought and salt tolerance in grapevine. Environ Exp Bot. 2023:**206**:105175. https://doi.org/10.1016/j.envexpbot.2022.105175

Wu FH, Chi Y, Jiang ZH, Xu YY, Xie L, Huang FF, Wan D, Ni J, Yuan F, Wu XM, et al. Hydrogen peroxide sensor HPCA1 is an LRR receptor kinase in *Arabidopsis*. Nature. 2020:**578**(7796):577–581. https://doi.org/10.1038/s41586-020-2032-3

Wu S, Liang D, Ma FW. Leaf micromorphology and sugar may contribute to differences in drought tolerance for two apple cultivars. Plant Physiol Biochem. 2014b:**80**:249–258. https://doi.org/10.1016/j.plaphy.2014.04.012

Wu GA, Prochnik S, Jenkins J, Salse J, Hellsten U, Murat F, Perrier X, Ruiz M, Scalabrin S, Terol J, et al. Sequencing of diverse mandarin, pummelo and orange genomes reveals complex history of admixture during citrus domestication. Nat Biotechnol. 2014a:**32**(7):656–662. https://doi.org/10.1038/nbt.2906

Wu QS, Srivastava AK, Zou YN. AMF-induced tolerance to drought stress in citrus: a review. Sci Hortic. 2013:**164**:77–87. https://doi.org/10.1016/j.scienta.2013.09.010

Wu Q, Wang M, Shen J, Chen D, Zheng Y, Zhang W. *ZmOST1* mediates abscisic acid regulation of guard cell ion channels and drought stress responses. J Integr Plant Biol. 2019:**61**(4):478–491. https://doi.org/10.1111/jipb.12714

Xie YP, Bao CN, Chen PX, Cao FG, Liu XF, Geng DL, Li ZX, Li XW, Hou N, Zhi F, et al. Abscisic acid homeostasis is mediated by feedback regulation of MdMYB88 and MdMYB124. J Exp Bot. 2021:**72**(2): 592–607. https://doi.org/10.1093/jxb/eraa449

Xu YY, Zeng RF, Zhou H, Qiu MQ, Gan ZM, Yang YL, Hu SF, Zhou JJ, Hu CG, Zhang JZ. Citrus FRIGIDA cooperates with its interaction partner dehydrin to regulate drought tolerance. Plant J. 2022b:**111**(1):164–182. https://doi.org/10.1111/tpj.15785

Xu X, Zhang Q, Gao X, Wu G, Wu M, Yuan Y, Zheng X, Gong Z, Hu X, Gong M, et al. Auxin and abscisic acid antagonistically regulate ascorbic acid production via the SlMAPK8-SlARF4-SlMYB11 module in tomato. Plant Cell. 2022a:**34**(11):4409–4427. https://doi.org/10.1093/plcell/koac262

Yang BH, Fu PN, Lu J, Ma FW, Sun XY, Fang YL. Regulated deficit irrigation: an effective way to solve the shortage of agricultural water for horticulture. Stress Biol. 2022a:**2**(1):28. https://doi.org/10.1007/s44154-022-00050-5

Yang J, Wang M, Zhou SS, Xu BY, Chen PH, Ma FW, Mao K. The ABA receptor gene MdPYL9 confers tolerance to drought stress in transgenic apple (*Malus domestica*). Environ Exp Bot. 2022b:**194**:104695. https://doi.org/10.1016/j.envexpbot.2021.104695

Yang JJ, Zhang J, Li C, Zhang Z, Ma FW, Li MJ. Response of sugar metabolism in apple leaves subjected to short-term drought stress. Plant Physiol Biochem. 2019:**141**:164–171. https://doi.org/10.1016/j.plaphy.2019.05.025

Yoshida T, Fujita Y, Maruyama K, Mogami J, Todaka D, Shinozaki K, Yamaguchi-Shinozaki K. Four *Arabidopsis* AREB/ABF transcription factors function predominantly in gene expression downstream of SnRK2 kinases in abscisic acid signalling in response to osmotic stress. Plant Cell Environ. 2015:**38**(1):35–49. https://doi.org/10.1111/pce.12351

Yu Y, Jia TR, Chen XM. The 'how' and 'where' of plant microRNAs. New Phytol. 2017:**216**(4):1002–1017. https://doi.org/10.1111/nph.14834

Yuan F, Yang HM, Xue Y, Kong DD, Ye R, Li CJ, Zhang JY, Theprungsirikul L, Shrift T, Krichilsky B, et al. OSCA1 mediates osmotic-stress-evoked Ca^{2+} increases vital for osmosensing in *Arabidopsis*. Nature. 2014:**514**(7522):367–371. https://doi.org/10.1038/nature13593

Zhang YF, Wang JY, Li YY, Zhang ZH, Yang LL, Wang M, Zhang YN, Zhang J, Li CA, Li L, et al. Wheat TaSnRK2.10 phosphorylates TaERD15 and TaENO1 and confers drought tolerance when overexpressed in rice. Plant Physiol. 2023:**191**(2):1344–1364. https://doi.org/10.1093/plphys/kiac523

Zhang MF, Wang JQ, Liu RL, Liu H, Yang HB, Zhu Z, Xu R, Wang P, Deng X, Xue S, et al. CsMYB96 confers resistance to water loss in citrus fruit by simultaneous regulation of water transport and wax biosynthesis. J Exp Bot. 2022b:**73**(3):953–966. https://doi.org/10.1093/jxb/erab420

Zhang H, Zhu J, Gong Z, Zhu JK. Abiotic stress responses in plants. Nat Rev Genet. 2022a:**23**(2):104–119. https://doi.org/10.1038/s41576-021-00413-0

Zhang Y, Zhu J, Khan M, Wang Y, Xiao W, Fang T, Qu J, Xiao P, Li CL, Liu JH. Transcription factors *ABF4* and *ABR1* synergistically regulate amylase-mediated starch catabolism in drought tolerance. Plant Physiol. 2022c:**191**(1):591–609. https://doi.org/10.1093/plphys/kiac1428

Zhou K, Li Y, Hu LY, Zhang JY, Yue H, Yang S, Liu Y, Gong X, Ma FW. Overexpression of *MdASMT9*, an N-acetylserotonin methyltransferase gene, increases melatonin biosynthesis and improves water-use efficiency in transgenic apple. Tree Physiol. 2022:**42**(5):1114–1126. https://doi.org/10.1093/treephys/tpab157

Zhu JK. Abiotic stress signaling and responses in plants. Cell. 2016:**167**(2):313–324. https://doi.org/10.1016/j.cell.2016.08.029

Zuazo VHD, Garcia-Tejero IF, Rodríguez BC, Tarifa DF, Ruiz BG, Sacristán PC. Deficit irrigation strategies for subtropical mango farming. A review. Agron Sustain Dev. 2021:**41**(1):13. https://doi.org/10.1007/s13593-021-00671-6

Zuo BX, Zheng XD, He PL, Wang L, Lei Q, Feng C, Zhou J, Li Q, Han ZH, Kong J. Overexpression of *MzASMT* improves melatonin production and enhances drought tolerance in transgenic *Arabidopsis thaliana* plants. J Pineal Res. 2014:**57**(4):408–417. https://doi.org/10.1111/jpi.12180