



Fruit crops combating drought: Physiological responses and regulatory pathways

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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 (Ca²⁺) 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 (Faghieh 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

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- 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 (Cyt f), 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 PSI

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 Shahsavari 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 (Świądrych 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

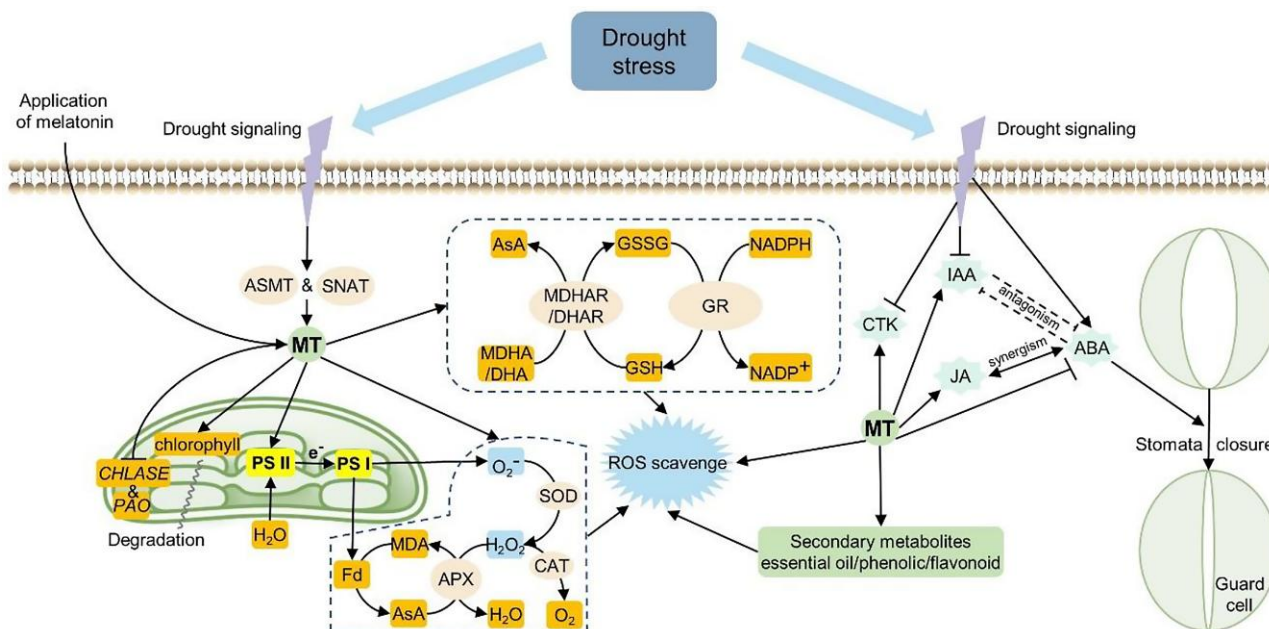


Figure 1. The role of melatonin in the drought stress response of fruit crops. Under drought, the MT content is enhanced by the application of exogenous MT and the overexpression of ASMT and SNAT. MT protects PSII and reduces the regulation of chlorophyll by repressing the expression of CHLASE and PAO. 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 respond to 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; PS I/II, photosystem I/II; Fd, ferredoxin; MDA, monodehydroascorbate; 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- μ M 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

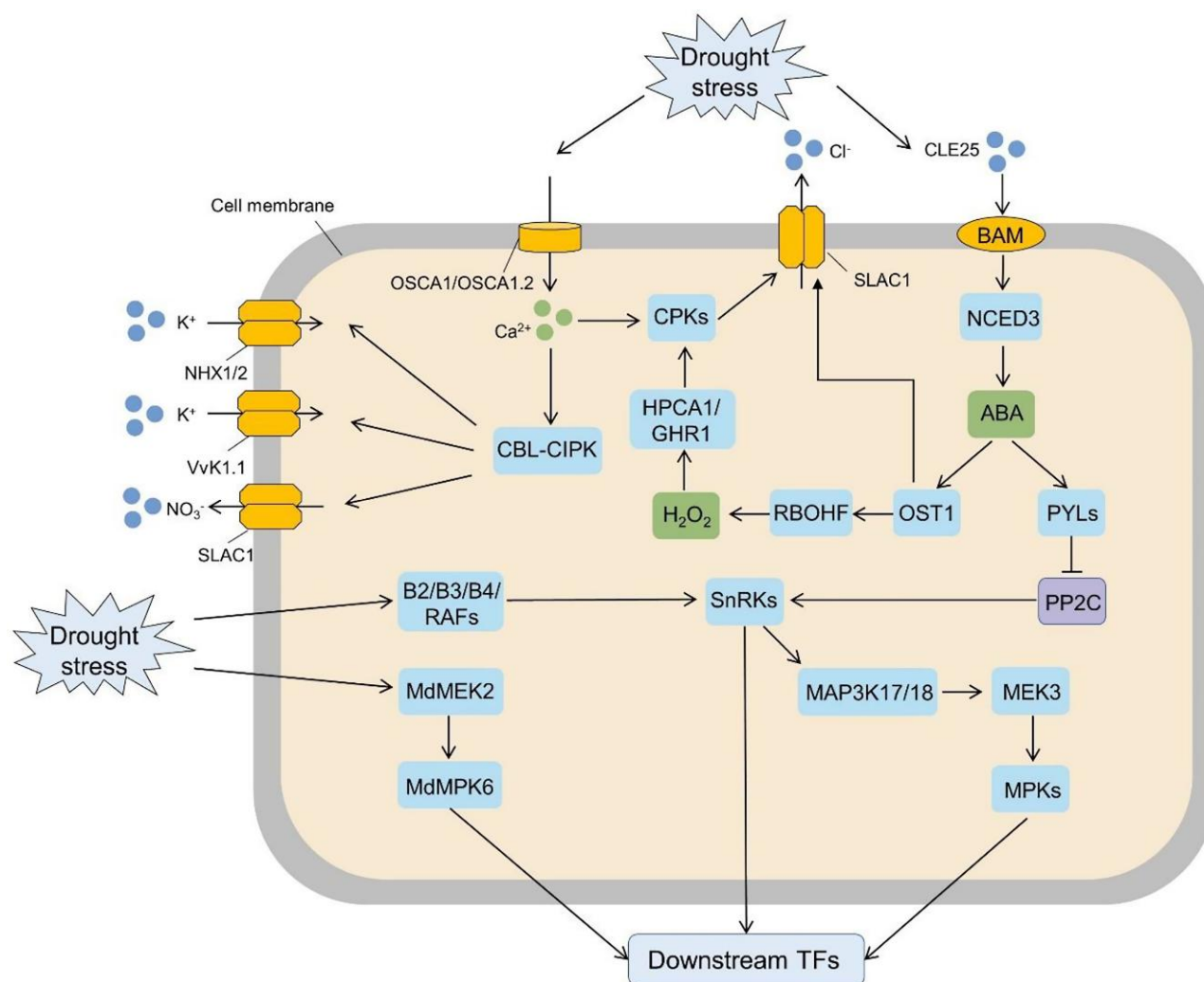


Figure 2. The sensing and signaling mechanisms of drought stress in plants. Drought is likely perceived as a decline in osmotic potential, which is sensed by the Ca^{2+} channel OSCA1 or OSCA1.2, causing the transport of Ca^{2+} into cells. The downstream signaling responses are thus mediated. The drought 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). H₂O₂ is likely sensed by GUARD CELL HYDROGEN PEROXIDE-RESISTANT1 (GHR1) (Hua et al. 2012) and the leucine-rich repeat receptor kinase HYDROGEN PEROXIDE-INDUCED Ca²⁺ INCREASE 1 (HPCA1) (Wu et al. 2020) to generate Ca²⁺ 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 (MAP3K/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

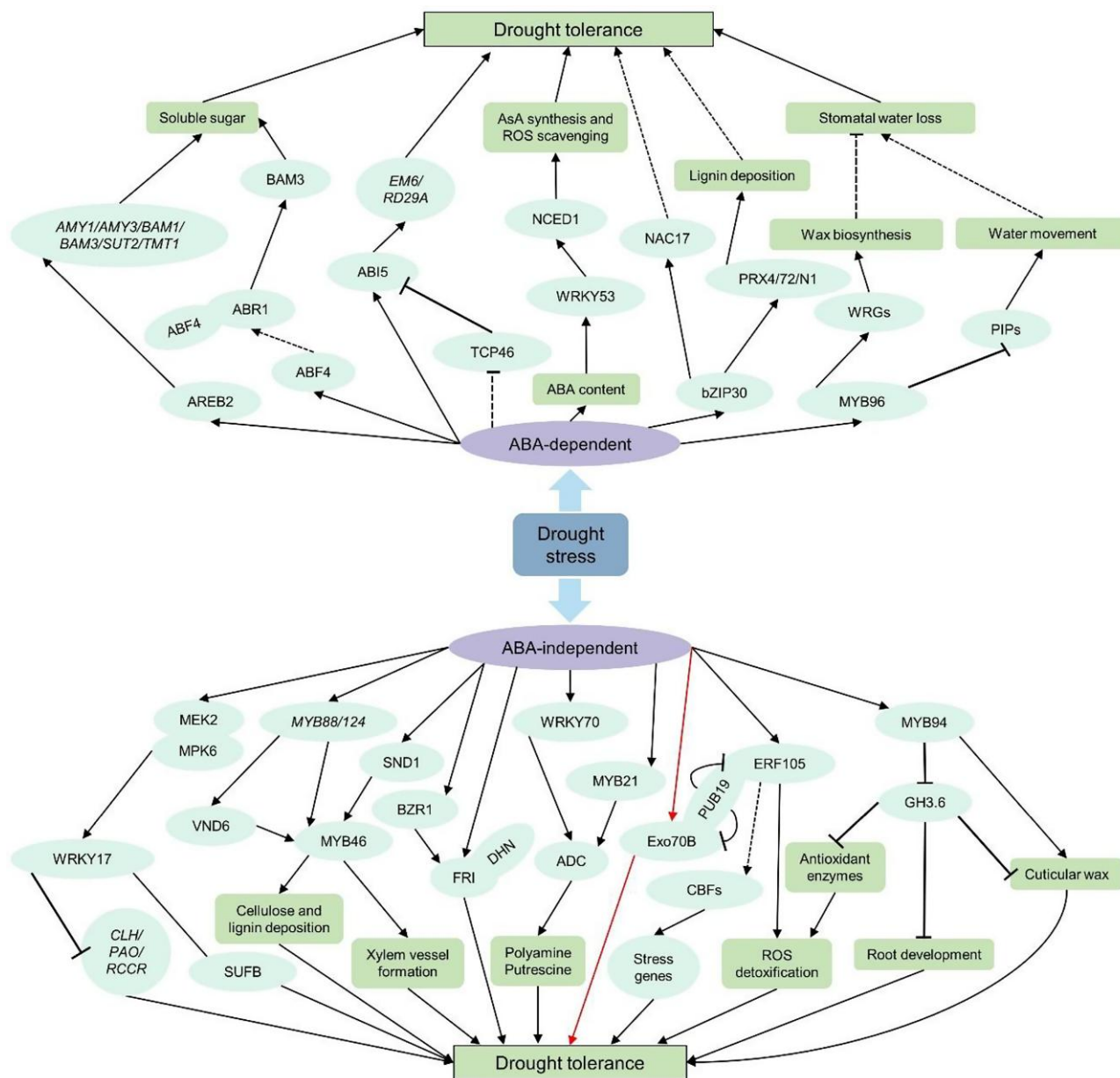


Figure 3. ABA-dependent and ABA-independent transcriptional regulatory pathways in fruit crops under drought stress. The solid arrows refer to direct effects, blocked arrows refer to inhibition, the dashed lines refer to indirect effects or unknown effects, and the red solid arrows refer to the regulation 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; 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 *MdSUF6*, a gene encoding a member of sulfur mobilization system, and indirectly downregulates chlorophyll catabolic genes (chlorophyllase (*MdCLH*), pheide 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 *MdSUF6* 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 transacting 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.

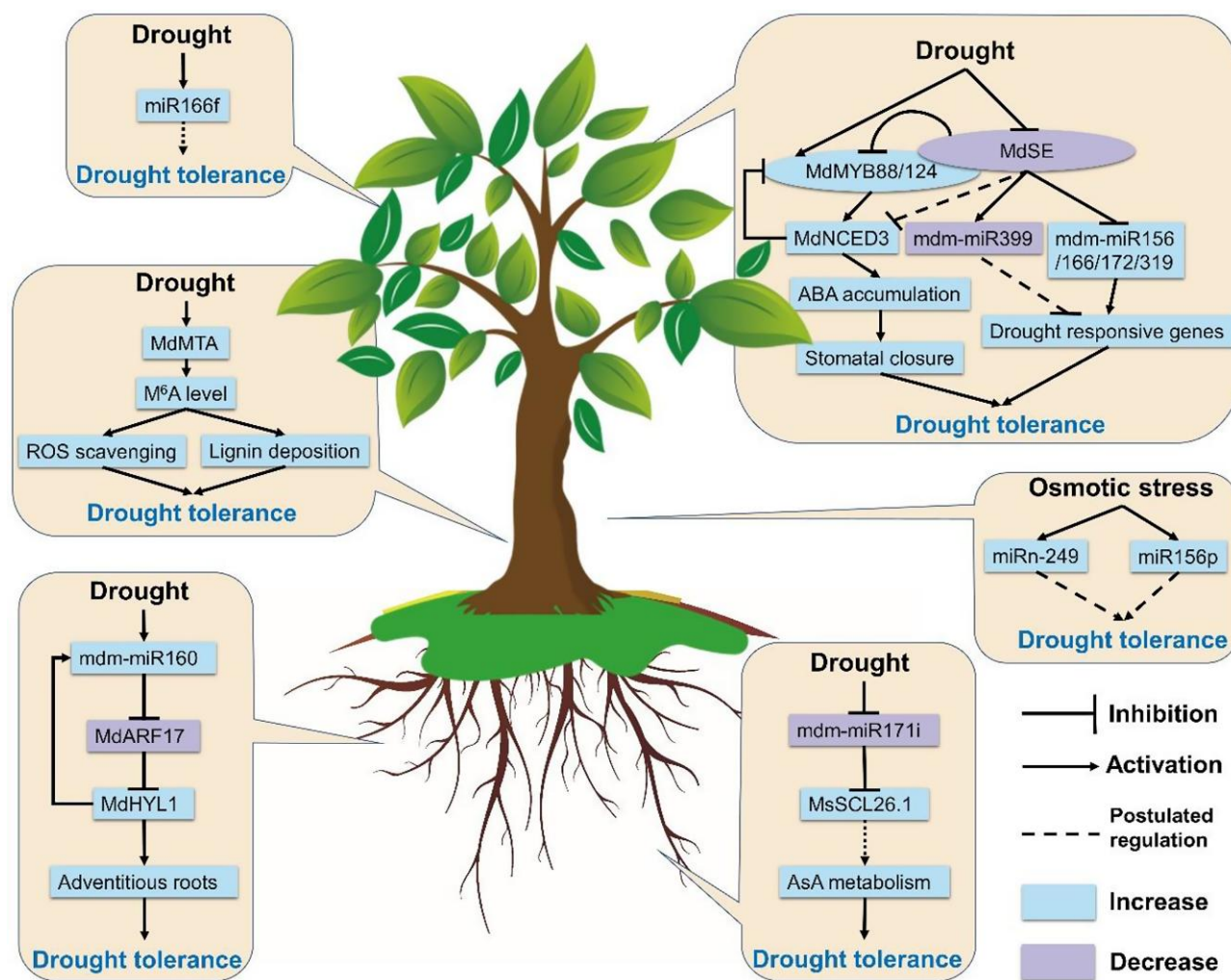


Figure 4. The regulatory roles of microRNAs (miRNAs) in fruit crops combating drought stress. The miR156p, miRn-249, mdm-miR160, mdm-miR171i, and miR166f respond to drought stimuli via regulating downstream genes. In addition, drought inhibits MdSE, which activates mdm-miR399 and inhibits mdm-miR156, 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; M⁶A, N⁶-methyladenosine; ROS, reactive oxygen species; ARF, AUXIN RESPONSE FACTOR; HYL, HYPOPLASTIC 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 N⁶-methyladenosine (m⁶A, the most common RNA modification) (Meyer et al. 2012). Drought stress induces the expression of MdMTA to increase the m⁶A 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 m⁶A 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 adaptation 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

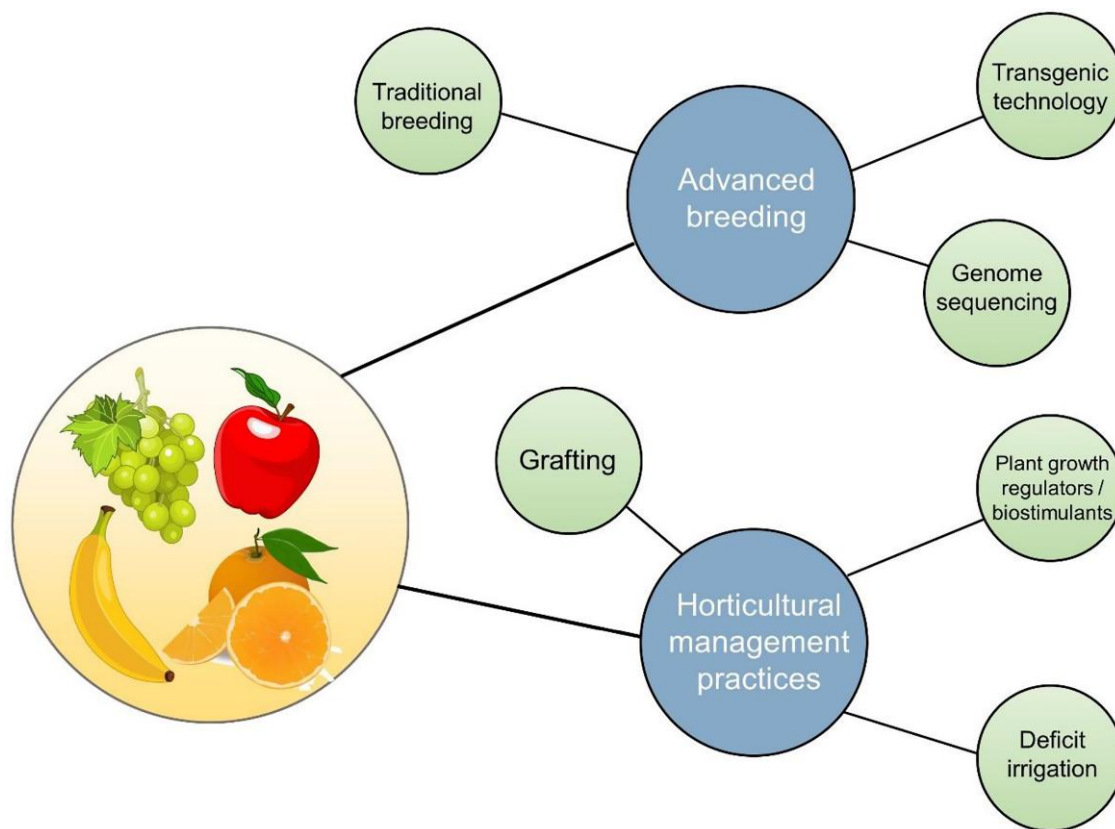


Figure 5. Strategies for overcoming drought in fruit crops. There are two strategies to reduce drought stress in fruit crops. One is advanced breeding, including traditional breeding, transgenic technology, and genome sequencing. Another is horticultural management practices, including grafting onto 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.

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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.

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