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REVIEW PAPER

The role of abscisic acid in fruit ripening and responses to abiotic stress

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Abstract

The phytohormone abscisic acid (ABA) plays a crucial role not only in fruit development and ripening, but also in adaptive responses to biotic and abiotic stresses. In these processes, the actions of ABA are under the control of complex regulatory mechanisms involving ABA metabolism, signal transduction, and transport. The endogenous ABA content is determined by the dynamic balance between biosynthesis and catabolism, processes which are regulated by 9-*cis*-epoxycarotenoid dioxygenase (NCED) and ABA 8′-hydroxylase (CYP707A), respectively. ABA conjugation by cytosolic UDP-glucosyltransferases, or release by β-glucosidases, is also important for maintaining ABA homeostasis. Recently, multiple putative ABA receptors localized at different subcellular sites have been reported. Among these is a major breakthrough in the field of ABA signalling—the identification of a signalling cascade involving the PYR/PYL/RCAR protein family, the type 2C protein phosphatases (PP2Cs), and subfamily 2 of the SNF1-related kinases (SnRK2s). With regard to transport, two ATP-binding cassette (ABC) proteins and two ABA transporters in the nitrate transporter 1/peptide transporter (NRT1/PTR) family have been identified. In this review, we summarize recent research progress on the role of ABA in fruit ripening, stress response, and transcriptional regulation, and also the functional verification of both ABA-responsive and ripening-related genes. In addition, we suggest possible commercial applications of genetic manipulation of ABA signalling to improve fruit quality and yields.

Key words: ABA, ABA metabolism, ABA signalling, ABA transporter, fruit ripening, stress response, transcriptional regulation.

Introduction

Fruits are rich sources of vitamins and minerals, both of which are important in human nutrition (DellaPenna and Pogson, 2006). The fleshy fruits have classically been divided into two categories based on their patterns of respiration during fruit maturation and ripening. One group is the climacteric fruits, which includes tomato, apple, pear, peach, and banana, fruits that are characterized by a burst of ethylene release during ripening (Buesa *et al.*, 1994; White, 2002; Hiwasa *et al.*, 2003; Zaharah *et al.*, 2013). In these fruits, ethylene induces the transcription of many ripening-associated genes, and its action results in the specific features of fruit ripeness (Bleecker and Kende, 2000; Giovannoni, 2001, 2004). The second group is the non-climacteric fruits, in which there is no respiration peak or ethylene burst during the ripening process, as shown in grapes (Deytieux *et al.*, 2007; Koyama *et al.*, 2010), strawberry (Trainotti *et al.*, 2005), cherry (Kondo and Inoue, 1997), and orange (Rodrigo *et al.*, 2006). Some fruits such as persimmon (*Diospyros kaki* Thunb.) are classified as climacteric (Abeles *et al.*, 1992), but, unlike typical climacteric fruits, the amount of ethylene released by the fruits declines as fruit ripening progresses (Fig. 1C). Ethylene released from ripe fruit at the harvest stage is <10% of that released by the immature fruit (Takata *et al.*, 1983; Nakano *et al.*, 2003).

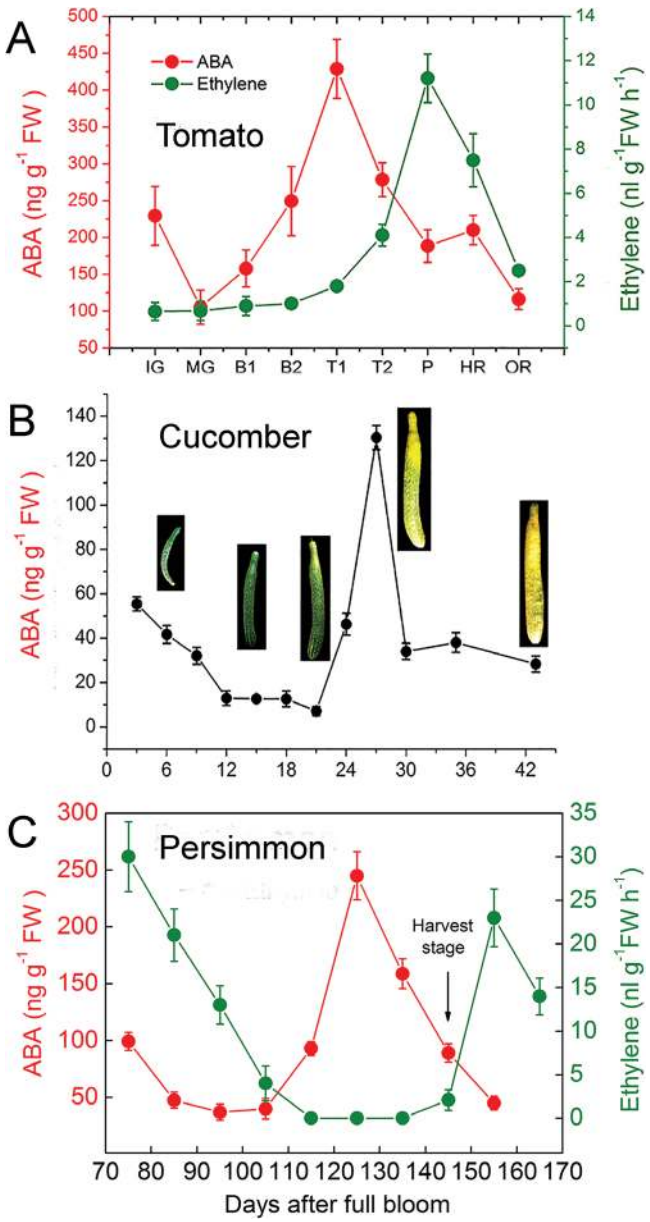

Fig. 1. Changes in ABA content and ethylene release in fruits of tomato (a climacteric fruit), cucumber (a non-climacteric fruit), and persimmon (an atypical climacteric fruit) during development and ripening. (A) During development of tomato fruit (cv. 'Jia Bao'), fruits were sampled at the following times after anthesis (stages): 20 DAA (immature green), 35 DAA (mature green), 38 DAA (breaker), 40 DAA (turning), 42 DAA (pink), 43 DAA (harvest red), and 45 DAA (over red) (Sun *et al.*, 2012a, b). (B) Based on the changes in growth parameters (Wang *et al.*, 2012), we defined the growth stages for Jin Qing NO. 1 cucumber fruit. From pollination to 9 days after flowering (DAF) was the immature green stage, 12–15 DAF was the breaker stage, 18–24 DAF was the turning stage, 27–30 DAF was the fully ripe stage, and 35–43 DAF was the senescence stage. (C) Fruit samples were collected from 75 days after full bloom (DAFB) to 165 DAFB. 115 DAFB was the onset of pigmentation, 125 DAFB at the ABA peak value was the turning stage, and 145 DAFB was the harvest stage (Zhao *et al.*, 2012).

To date, the ripening mechanism of climacteric fruits, especially with respect to the effects of ethylene, has been well studied (Alexander and Grierson, 2002; Klee and Giovannoni, 2011). A high-level regulatory network of transcription factors that control fruit development has been described in tomato (Vrebalov *et al.*, 2002; Srivastava and Handa, 2005; Manning *et al.*, 2006; Seymour *et al.*, 2008, 2013a, 2013b; Itkin *et al.*, 2009; Chung *et al.*, 2010; Jaakola *et al.*, 2010; Karlova *et al.*, 2011; Martel *et al.*, 2011; Lee *et al.*, 2012). In contrast, the mechanisms involved in the ripening of non-climacteric fruits remain unclear. Although the patterns of fruit development and ripening are diverse, they exhibit the same ripening phenomena which usually include cell wall modifications together with associated fruit softening, the synthesis of pigments, the conversion of starch into simple sugars, and the synthesis of volatile compounds that influence fruit taste and aroma (Saladie *et al.*, 2007). Accompanying these biochemical processes, fruits go through a remarkable transformation from something that is unpalatable into an attractive, edible fruit (Barry *et al.*, 2010; Matas *et al.*, 2011). The difference between climacteric and non-climacteric fruits depends only on whether ethylene is released during maturation/ripening or not. In addition, studies on rare tomato mutations such as ripening inhibitor (*rin*) and non-ripening (*nor*) have shown that application of exogenous ethylene does not promote fruit ripening, yet it does induce expression of ethylene-regulated ripening genes (Tigchelaar *et al.*, 1978; Yen *et al.*, 1997). These results indicate that in addition to general ethylene biosynthesis and signalling, there may be other ethylene-independent regulatory factors responsible for the control of ripening of both fruit types that are upstream of ethylene.

Abscisic acid (ABA) can be considered to be another ripening control factor for the following reasons: (i) as shown in Fig. 1, there is a sharp increase in ABA accumulation during the onset of fruit ripening and/or the ripening process in both climacteric (Buesa *et al.*, 1994) and non-climacteric (Kojima *et al.*, 1995; Kondo and Inoue, 1997) fruits; (ii) ABA accumulates preceding ethylene release in climacteric fruits (Zhang *et al.*, 2009a, b); (iii) the application of exogenous ABA enhances the production of several metabolites involved in fruit ripening, thereby promoting fruit ripening (Chernys and Zeevaart, 2000; Ban *et al.*, 2003; Cakir *et al.*, 2003; Jeong *et al.*, 2004; Giribaldi *et al.*, 2010); (iv) in ABA-deficient tomato mutants, the fruit did not show the normal growth pattern observed in the wild type (Taylor *et al.*, 2000; Galpaz *et al.*, 2008); (v) the de-greening stage began later in ABA-deficient orange mutants (Rodrigo *et al.*, 2003); and (vi) the inhibition of ABA signalling in *FaPYL1*-RNA interference (RNAi)-silenced strawberry fruit impeded fruit ripening (Jia *et al.*, 2011). ABA was first discovered to function in plant wilting and stomatal closure in the late 1960s (Mittelheuser and Van Steveninck, 1969; Wright and Hiron, 1969). To date, considerable progress has been made in research into the role of ABA in the regulation of fleshy fruit ripening. However, the molecular mechanisms remain to be elucidated. To describe the mechanisms of ABA action at the molecular level, it is necessary to identify all of the components involved in ABA homeostasis, including the functional components in ABA metabolism, signal transduction, and transport. On the other hand, ABA is associated with the plant's response to different kinds of abiotic stresses such as drought, high temperature, chilling, and salinity (Qin and Zeevaart, 2002; Seki

et al., 2007). However, research on the involvement of ABA in regulating abiotic stress in fruits has rarely been reported.

This review focuses on research progress into the role of ABA in fruit ripening and responses to abiotic stress.

Synthesis, catabolism, and reactivation of ABA in fruits

In higher plants, the ABA biosynthetic pathway is well understood (Fig. 2), and numerous mutants have been identified at each step in this pathway in *Arabidopsis* (North *et al.*, 2007; Huo *et al.*, 2013), tomato (Burbidge *et al.*, 1999; Nitsch *et al.*, 2009), and maize (Tan *et al.*, 1997, 2001). ABA is synthesized *de novo* from a C_{40} carotenoid. The carotenoid biosynthetic pathway begins with the formation of phytoene from two molecules of geranylgeranyl diphosphate (GGPP) in the central isoprenoid pathway. Four desaturation steps give rise to lycopene; cyclizations at both ends of the lycopene molecule produce α- or β-carotene, which undergo hydroxylation at C3 and C3′ to form the xanthophylls, lutein and zeaxanthin, respectively. An important phase of ABA biosynthesis is initiated in plastids with the hydroxylation and epoxidation of the β-carotene to produce the all-*trans*-xanthophylls zeaxanthin and violaxanthin. Violaxanthin is then converted into 9-*cis*-epoxyxanthophylls, which are oxidatively cleaved by 9-*cis*-epoxycarotenoid dioxygenase (NCED) to yield xanthoxin, the first C_{15} intermediate of ABA biosynthesis. Xanthoxin exits the plastid into the cytosol where it is oxidized in two further steps to form ABA (Qin and Zeevaart, 1999; Schwartz *et al.*, 2003; Taylor *et al.*, 2005). Overexpression experiments in transgenic plants demonstrated unequivocally that NCED is a key rate-limiting step in ABA biosynthesis (Thompson *et al.*, 2000; Iuchi *et al.*, 2001; Tung *et al.*, 2008). The ABA catabolic pathway has been established through the hydroxylation reaction. In the hydroxylation pathway, among three different methyl groups, C-8′ is the predominant position for the hydroxylation reaction, which is mediated in *Arabidopsis* by proteins encoded by the *CYP707A* gene family (Kushiro *et al.*, 2004; Saito *et al.*, 2004). Dihydroxyphaseic acid (DPA) may be the major metabolite of ABA (Setha *et al.*, 2005). Moreover, ABA conjugation by cytosolic UDP-glucosyltransferases (GTs) or release by β-glucosidases (BGs), through intracellular or intertissue transport processes, can also alter ABA homeostasis (Hartung *et al.*, 2002; Sauter *et al.*, 2002; Jiang and Hartung, 2008; Seo and Koshiba, 2011;

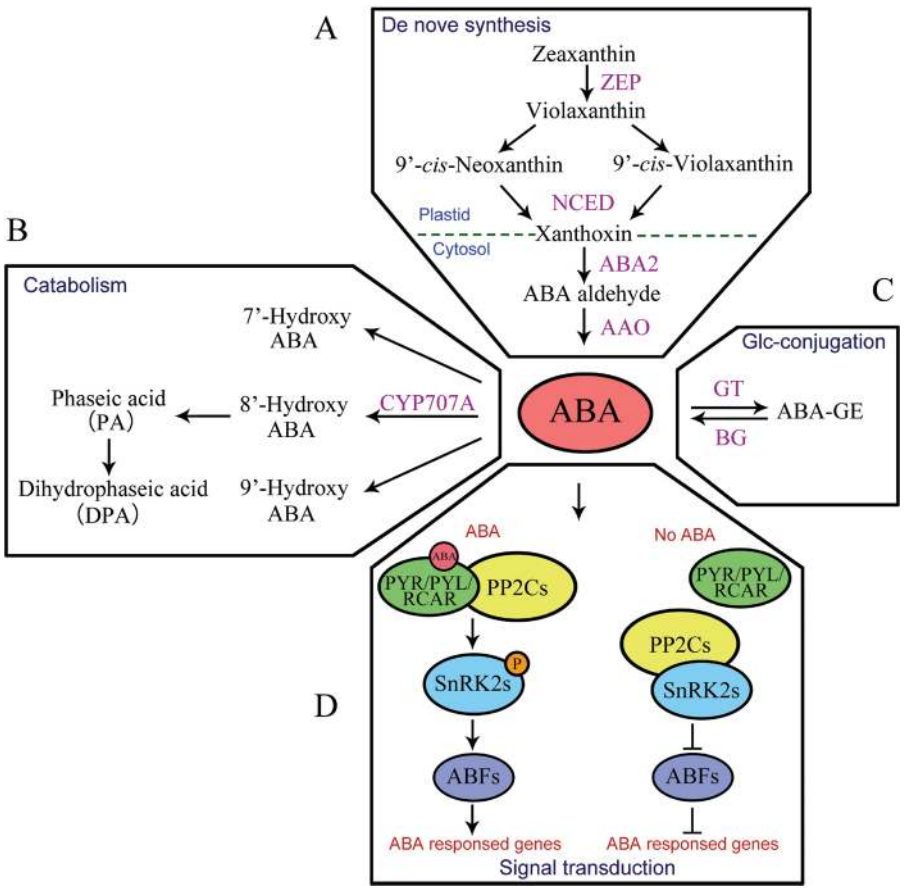

Fig. 2. ABA metabolism, signal transduction, and reactivation pathways. (A) ABA is synthesized *de novo* from a C_{40} carotenoid (Qin and Zeevaart, 1999; Schwartz *et al.*, 2003; Taylor *et al.*, 2005). (B) ABA catabolic pathway (Saito *et al.*, 2004; Kushiro *et al.*, 2004; Setha *et al.*,2005). (C) ABA–glucose conjugation (Sauter *et al.*, 2002; Seo and Koshiba, 2011; Burla *et al.*, 2013). (D) ABA signal transduction (Ma *et al.*, 2009; Park *et al.*, 2009; Yin *et al.*, 2009; Gonzalez-Guzman *et al.*, 2012).

Burla *et al.*, 2013). Thus, free ABA, phaseic acid, and DPA are present mainly in the extravacuolar compartments. In contrast to these oxidized ABA catabolites, ABA-glucosyl ester has been reported to accumulate in vacuoles and presumably in the endoplasmic reticulum, since AtBG1 is located there (Lee *et al.*, 2006; Xu *et al.*, 2012).

In fruit, the endogenous ABA content is determined by the dynamic balance of biosynthesis (*NCED* genes), catabolism (*CYP707A* genes), and reactivation (*BG*/*GT* genes), and the spatio-temporal expression of the genes encoding these proteins is regulated by the ABA pool at the transcriptional level. Therefore, the change in the dynamic balance of these three processes may lead to alterations in the level of ABA. Since the gene encoding NCED, the key ABA biosynthesis enzyme, was first isolated from the maize *vp14* mutant (Tan *et al.*, 1997), it has been cloned and characterized from various climacteric fruit species such as apple (Lara and Vendrell, 2000), peach (Alvaro *et al.*, 2013), tomato (Burbidge *et al.*, 1999), and melon (Sun *et al.*, 2013), as well as non-climacteric fruits such as orange (Rodrigo *et al.*, 2006) and grape (Wheeler *et al.*, 2009). At present, at least four *NCED* genes have been cloned from tomato fruits (Huo *et al.*, 2013). ABA levels in tomato fruit are regulated mainly by *SlNCED1* at the transcriptional level, and in response to dehydration (Zhang *et al.*, 2009a). Tomatoes overexpressing *SlNCED1* had enhanced ABA accumulation and drought tolerance, and reduced levels of transpiration (Thompson *et al.*, 2000). Tomato fruits from an ABA-deficient mutant showed a decrease in mean fruit weight and did not show the normal development and ripening observed in the wild type (Galpaz *et al.*, 2008). Also, in transgenic tomato fruits expressing a *SlNCED1*-RNAi construct, as a consequence of silencing the *SlNCED1* gene, the reduction in endogenous ABA levels inhibited cell wall degradation, indicating that ABA is indispensable during fruit development and ripening (Sun *et al.*, 2012a, b).

On the other hand, the regulation of *CYP707A*, which encodes ABA 8′-hydroxylase, can alter the dynamic balance of ABA levels (Saito *et al.*, 2004). For example, enhanced expression or loss of function of the *CYP707A2* gene can affect ABA levels in *Arabidopsis* seedlings, which will subsequently change their sensitivity to exogenous glucose (Zhu *et al.*, 2011). The *PacCYP707A1* and *PacCYP707A3* genes expressed in sweet cherry fruit are up-regulated by water stress and ABA treatment (Ren *et al.*, 2010). It is worth noting that the regulatory mechanisms of *CYP707A* gene expression in response to ABA and dehydration are somewhat different. Although ABA-responsive elements (ABREs) are present in the *CYP707A* gene promoter regions, in ABA-deficient (*aba2-2* and *nced3-2*) or ABA-insensitive (*abi1-1* and *abi2-1*) mutants, the responses of *CYP707A* genes to dehydration are ABA independent, but sometimes depend partly on ABA signalling under dehydration conditions (Umezawa *et al.*, 2006). Besides these main regulatory steps in the ABA metabolic pathway, metabolic steps upstream of ABA metabolism also contribute to the determination of ABA levels. Overexpression of genes encoding regulatory enzymes in the methylerythritol phosphate (MEP) pathway (1-deoxy-D-xylulose 5-phosphate synthase), the carotenoid biosynthesis pathway (phytoene synthase), and the xanthophyll cycle (*ZEP*) can cause enhanced accumulation of ABA in seeds or seedlings (Frey *et al.*, 1999; Estévez *et al.*, 2001; Lindgren *et al.*, 2003). Taken together, this indicates that the regulation of ABA metabolism is not merely restricted to specific steps in ABA metabolism (i.e. *NCED* and *CYP707A*), but is also coordinated with other pathways that are upstream of ABA metabolism.

In addition, reactivation of the BG-conjugated/inactive ABA to free/active ABA also affects cellular ABA levels (Price *et al.*, 2003; Burla *et al.*, 2013). Recently, the functions of BGs in the activation of hormone groups in plants, including auxins, ABA, and cytokinins, has been reported (Brzobohaty *et al.*, 1993; Lee *et al.*, 2006). One or more genes in the BG family can have expression patterns that coincide with the variation in ABA accumulation during fruit ripening, which may indicate their roles in co-regulating the ABA pool in these fruits at the transcriptional level (Sun *et al.*, 2010; Zhang *et al.*, 2013). For example, in strawberry fruit, the expression pattern of *FaBG3* was coincident with ABA accumulation during fruit ripening, and it has been shown by gene silencing (*FaBG3*-RNAi plants) that *FaBG3* is not only related to fruit ripening, but can also confer disease resistance in strawberry (Li *et al.*, 2013). GT is implicated in the presence or absence of a smoky aroma in tomato fruits. Recently, a NON-SMOKY GLYCOSYLTRANSFERASE1 (NSGT1) gene was identified in tomato (Tikunov *et al.*, 2013). Both BG and GT are members of large gene families, and their roles in the regulation of the ABA level during fruit ripening are still unclear. Further research is needed to identify and isolate the specific substrates for these enzymes in fruits.

ABA signal transduction and its transcriptional regulation

The ABA-mediated signalling cascade is initiated by perception of ABA through ABA receptors. In recent years, considerable progress has been made in studies of ABA signal transduction, and several different types of ABA receptors have been reported in the literature, including ABAR/CHLH (Mg-chelatase H subunit) (Mochizuki *et al.*, 2001; Shen *et al.*, 2006; Shang *et al.*, 2010) and the GPCR-type G proteins (Liu *et al.*, 2007; Pandy *et al.*, 2009). For these receptors, their exact nature and roles have not been confirmed, and are still the subject of some debate (Muller and Hansson, 2009; Wu *et al.*, 2009). Recently, a major breakthrough in the field of ABA signalling was achieved, which was the identification of the PYR/PYL/RCAR protein family, the type 2C protein phosphatases (PP2Cs), and subfamily 2 of the SNF1-related kinases (SnRK2*s*) (Ma *et al.*, 2009; Melcher *et al.*, 2009; Nishimura *et al.*, 2009; Park *et al.*, 2009; Santiago *et al.*, 2009; Yin *et al.*, 2009; Gonzalez-Guzman *et al.*, 2012). The current ABA signal transduction model can be described as follows (Fig. 2): in the absence of ABA, PP2Cs inhibit SnRK2s by physical interaction and through their phosphatase activity. Binding of an ABA molecule to the ABA receptor PYR/PYL/RCAR leads to structural changes in the receptor,

enabling the interaction of the ABA receptors with PP2Cs, thus disrupting the interaction between PP2Cs and SnRK2s. SnRK2s are released from the PP2C inhibition, and are able to activate their downstream targets, which include transcription factors as well as other targets, such as ABA-responsive element binding proteins (AREBs) and ABA-responsive element binding factors (ABFs) (Klingler *et al.*, 2010). AREB/ABFs are ABA-responsive transcription factors containing a basic leucine zipper family (bZIP)-type DNA-binding domain that binds the ABA-responsive element (T/CACGTGGC) and have a pivotal role in ABA-dependent gene activation (Choi *et al.*, 2000; Hattori *et al.*, 2002; Kang *et al.*, 2002; Gómez-Porras *et al.*, 2007). For example, AREB1, AREB2, ABF3, and ABF4 positively regulate the expression of ABA signalling response genes (Fujita *et al.*, 2009; Yoshida *et al.*, 2010). Potential perception of ABA through different types of receptors or by different members of the PYR/PYL/RCAR family raises several questions that have yet to be addressed, such as: what is the relative contribution of each type of receptor, and how do multiple inputs of perception integrate into ABA signalling? ABA in different subcellular compartments may require different ABA receptors to initiate ABA-mediated signalling. According to this scenario, it is possible that different physiological responses can be induced by ABA receptors which perceive different subcellular pools of ABA (Gonzalez-Guzman *et al.*, 2012). In recent years, considerable progress has been made in the understanding of ABA signal transduction pathways in fruits. There are a few transcription factors which are important for fruit ripening, and these have also been described as being related to the ABA response. For example, VvABF2, a grape bZIP transcription factor belonging to group A of bZIPs, has been reported. Overexpression of VvABF2 in grape cells resulted in up-regulation and/or modification of existing networks related to ABA responses, enhanced responses to ABA treatment, and changes in the synthesis of phenolic compounds and cell wall softening (Nicolas *et al.*, 2014). The *Fragaria xananassa* MYB10 transcription factor plays a general regulatory role in the flavonoid/phenylpropanoid pathway during ripening in strawberry fruit. The R2R3-MYB10 transcription factor expressed in strawberry fruit is repressed by auxins and activated by ABA, in parallel with the ripening process. This transcription factor regulates the expression of most of the early-regulated biosynthesisgenes (*EBG*s) and the late-regulated biosynthesisgenes (*LBG*s) which are involved in anthocyanin production in ripened fruit receptacles (Medina-Puche *et al.*, 2013). The R2R3-type transcription factor MYB30 is involved in the regulation of ABA signalling. Coordination of ABI5 and MYB30 sumoylation by SIZ1 may balance gene expression, which is required for regulation of ABA signalling during seed germination (Zhenga *et al.*, 2012). ABA production and PacMYBA expression work closely together to control anthocyanin biosynthesis in red-coloured sweet cherry pigmentation. Moreover, ABA might directly regulate *PacMYBA* expression at the transcriptional level (Shen *et al.*, 2014). In addition, there are other large groups of genes encoding transcription factors that could be important in fruit development; for instance, the bZIP genes have been shown to be involved in the control of nitrogen/carbon balance, and in the response to ABA (Nijhawan *et al.*, 2008; Lovisetto *et al.*, 2013). Different calcium-dependent protein kinases (CDPKs) could play a role in the control of ripening; an example is the protein kinase FvCDPK1 from wild diploid strawberry, which is expressed in fruits during ripening, and is up-regulated by ABA (Feng *et al.*, 2013). In each ABA signal gene family, there is only one or several genes with expression patterns that correspond to the variation in ABA content and are involved in fruit ripening (Gambetta *et al.*, 2010; Romero *et al.*, 2012). For example, in tomato, 14 *SlPYL* genes from the same gene family had different sensitivities to endogenous/exogenous ABA and drought (Sun *et al.*, 2011), showing that their individual regulation is complex. Although some *PYL*, *PP2C*, and *SnRK2* genes may not play roles in ABA signal transduction, they may have important functions in other biological processes (Schweighofer *et al.*, 2004; Gonzalez-Ballester *et al.*, 2008), and whether they are involved in ABA responses still needs to be investigated.

Transport of ABA

ABA metabolism, perception, and transport together allow plants to use ABA as a signalling molecule. Since ABA accumulation occurs in different tissues and cells, and ABA has systemic effects, a requirement for efficient intercellular transport of ABA has been proposed (Cheng *et al.*, 2002; Koiwai *et al.*, 2004; Endo *et al.*, 2008). Although ABA transport has long been demonstrated in plants, the first breakthroughs in the identification of plasma membrane-localized ABA transporters came in 2010, with the detection of two ATP-binding cassette (ABC) proteins. More recently, two ABA transporters in the nitrate transporter 1/peptide transporter (NRT1/PTR) family, which are involved in the transport of nitrogen compounds, have been described, and further work needs to be done to determine whether there is an interaction between ABA and nitrogen signalling or nutrition (Boursiac *et al.*, 2013). At present, the molecular cloning of ABA transporters and the phenotypes of their respective mutants genetically support the requirement of ABA transport for proper signalling throughout the plant. ABA is transported from the site of synthesis to the site of action, and where ABA receptors decode the message within a fruit is different from that in vegetative organs, because the morphological structure of fruit is unlike that of the root, stem, or leaf (Antoni *et al.*, 2011). Transport of ABA in fruits is mainly via the phloem. In the fruit of sweet cherry (*Prunus avium* L.), ABA was shown to be transported only in the phloem (Else *et al.*, 2004). The amount of ABA exported from the developing fruit was greatest during stone formation and the beginning of fruit expansion, and declined markedly as the fruit began to mature (Else *et al.*, 2004). Phloem export of ABA from developing fruit also decreased during the later stages of fruit ripening. This may reflect a general decrease in phloem export, but it could also contribute to the accumulation of ABA in the ripening fruit. Ripening of the sweet fruit is coordinated by ABA, and fruit concentrations rise markedly during the final stages of

maturity (Ren *et al.*, 2011). Phloem import of ABA into fruit significantly promoted ripening during the onset of ripening. For example, a 2-year-old shoot with fruit was cut when the fruit had become straw yellow. The shoot was then placed in a 1 mmol l^{-1} ABA solution in the laboratory, with an untreated control consisting of distilled water. Five days after the initiation of treatment, maturity index (SSC/TA), fruit softening, and anthocyanin levels were significantly increased with increasing ABA concentrations in the fruit (Luo *et al.*, 2013). This indicates that ABA is readily imported into fruits from the shoot during the onset of fruit ripening.

ABA regulation of metabolic pathways related to fruit ripening

There is evidence to support a role for ABA in photosynthate unloading from phloem in developing fruits. For example, ABA treatment enhanced the uptake of sugar into vacuoles in apple fruit flesh (Yamaki and Asakura, 1991), and increased the sugar content of developing citrus fruit (Kojima *et al.*, 1995). Sugar and ABA signalling have revealed intimate connections in sugar-insensitive and sugar-hypersensitive mutants of *Arabidopsis*. For example, many sugar mutants turn out to be allelic to known ABA-sensitive and ABA-insensitive mutants, such as *ABI3-5*, *ABF2-4*, and *ABA1-3* (Smeekens *et al.*, 2000; Gazzarrini and McCourt, 2001). ABA and sugar often exert similar or antagonistic effects on diverse developmental processes (Finkelstein and Gibson, 2002; Rolland *et al.*, 2006; Gambetta *et al.*, 2010). For example, supplementation with exogenous sugars is able to relieve the inhibition of seed germination caused by added ABA (Price *et al.*, 2003; Dekkers *et al.*, 2004). Recently, it has been found that the manipulation of endogenous sucrose content alters the expression of *FaNCED* genes and the content of endogenous ABA in strawberry fruit (Jia *et al.*, 2013). Even so, the complexity of fruit ripening and the potential role of ABA in this process indicates the presence of multiple signalling pathways that are influenced by hormone balance and sugar signalling.

ABA also regulates the anthocyanin biosynthetic pathway in fruit. ABA induces anthocyanin accumulation to make the fruit colour-up, and also participates in the activation of plant tissue defence against potential damage, apparently by triggering biosynthesis of phenols which filter out harmful radiation and also act as antioxidants (Lacampagne *et al.*, 2009). For example, during fruit development in bilberry (*Vaccinium myrtillus* L.), ABA levels and expression of *VmNCED1* and the neoxanthin synthase gene (*VmNSY*) increased sharply at the onset of ripening, the stage in which expression of the chalcone synthase (*VmCHS*) and anthocyanidin synthase genes (*VmANS*) also increases along with the accumulation of ABA (Karppinen *et al.*, 2013). Recent studies have also shown that the transcriptional regulators of structural genes in the phenylpropanoid and flavonoid pathways, as well as genes considered to be involved in the acylation and transport of anthocyanin into the vacuole, are up-regulated by ABA treatment in grape berries (Koyama *et al.*, 2010; Berli *et al.*, 2011).

ABA also participates in fruit texture formation. The cell walls in fruits are generally composed of cellulose microfibrils tethered with xyloglycans embedded in pectin mesh, and glycoproteins (Carpita and Gibeaut, 1993). Changes in the cell wall are associated with fruit softening, which is related to the expression of a number of hydrolase and transglycosylase genes (Huber, 1983), including increases in enzyme activity and mRNA levels of polygalacturonase (PG) (Smith and Gross, 2000), pectin methylesterase (PME) (Tieman *et al.*, 1992; Deytieux-Belleau *et al.*, 2008), endo-β-1,4-glucanases (Cels) (Lashbrook *et al.*, 1994), and expansin (Exp1) (Brummell *et al.*, 1999; Cosgrove *et al.*, 2000). Because ethylene has variable effects on the activities of these hydrolases during ripening (Nishiyama *et al.*, 2007), it is generally accepted that fruit softening is induced by ethylene. However, direct observation and molecular level evidence of the involvement of ABA in fruit softening has recently been provided (Sun *et al.*, 2012a, b). In *SlNCED1*-RNAi transgenic fruits, the pectin content was shown to be significantly higher, the shelf life was longer, and the pulp was firmer and more flexible than in control fruits during the ripening stage (Sun *et al.*, 2012a). Also the role of ABA in regulating these genes depended on the stage of fruit development.

In addition to ethylene, ABA also shows reciprocity with other phytohormones during fruit development. It has been demonstrated that auxin acts upstream of the major regulator of seed dormancy by recruiting the auxin response factors AUXIN RESPONSE FACTOR 10/16 to control the expression of ABI3 during seed germination (Liu *et al.*, 2013). In strawberry fruit, auxin promotes fruit expansion at the start of development; however, the ripening period is accompanied by a decrease in auxin levels, although endogenous ABA in both achenes and receptacles increased as the fruit ripened (Archbold and Dennis, 1984). Application of the synthetic auxin NAA (1- naphthaleneacetic acid) down-regulated the expression of *FaNCED* genes and reduced ABA accumulation during development and ripening of strawberry fruit (Ji *et al.*, 2012). ABA also regulates the development of abscission in the fruit/flower pedicel. In the apple (*Malus domestica*) fruitlet, a strong correlation between abscission and ABA levels in the fruit cortex was observed (Eccher *et al.*, 2014). During the early phases of the shedding process, major transcriptomic changes and metabolic rearrangements occur within the fruit. A metabolomic study identified isoprene as an early marker of abscission induction. According to the hypothetical model, ABA may transiently cooperate with other hormones and secondary messengers in the generation of an intra-fruit signal, which then leads to the downstream activation of the abscission zone (Eccher *et al.*, 2014).

Endogenous ABA variation also alters the production of carotenoids, which are precusor substrates for ABA biosynthesis (Kachanovsky *et al.*, 2012). In the tomato mutants high-pigment 3 (*hp3*) and high-pigment 2 (*hp2*), the fruits are redder in colour than are the control fruits (Bino *et al.*, 2005; Kolotilin *et al.*, 2007; Galpaz *et al.*, 2008). The tomato *hp3* mutant contains an altered gene for zeaxanthin epoxidase (*Zep*), which catalyses the conversion of zeaxanthin to violaxanthin and neoxathin. The levels of lycopene and β-carotene

were increased due to the up-regulation of phytoene synthase (*SlPSY1*), a rate-limiting enzyme (Fraser *et al.*, 2002), and down-regulation of lycopene β-cyclase (*SlBcyc*) expression in the *SlNCED1*-RNAi lines compared with the control fruit (Sun *et al.*, 2012a,b). An alternative explanation of why the transgenic fruit contained more carotenoids could be that the carbon flux, which normally channels carbon to free ABA and ABA metabolite accumulation during ripening, is partially blocked by a significant reduction in NCED activity. The 'backlogged' carbon is then shunted to the carotenoid pathway in the RNAi lines, resulting in the increased biosynthesis and accumulation of upstream compounds in the pathway, mainly lycopene and β-carotene.

Regulating the effect of ABA during abiotic stress in fruits

Fruits possess an adversity monitoring system. When fruits experience environmental stresses, they can launch a variety of reactions through signal transduction, thereby avoiding the impact or harm caused by abiotic stress. On a broader scale, ABA is a stress-related signalling molecule, and the main function of ABA in plants is to regulate water balance and osmotic stress tolerance (Cakir *et al.*, 2003). The accumulation of ABA in fruits has been shown to correlate with abiotic stresses (Deluc et al., 2007, 2009). For example, the persimmon fruit has a large calyx which adheres to the fruit throughout ripening, and the response of the calyx lobes to the stress of water loss was more rapid than that observed in the fruit (Leng *et al.*, 2009; Zhao *et al.*, 2012). We propose a persimmon softening model in which the *DKNCED1* gene initiates ABA biosynthesis in the dehydrating calyxes of fruits: (i) ABA may induce ethylene biosynthesis via the regulation of *ACS* and *ACO* gene expression; and (ii) the ethylene produced diffuses into the pulp of the fruit, where autocatalytic ethylene biosynthesis is induced and results in an abrupt increase in ethylene production and fruit softening. In cherry, fruits have a long pedicel that contains large numbers of stomates, which are the site for gas exchange nearest the developing fruit. The evaporation of water from cherry fruit occurs mainly through the stomata on the pedicels (Luo *et al.*, 2013). The ABA peak occurred sooner than did the ethylene peak in the pedicels post-harvest. The peak values for ABA, ethylene release, and the expression of related genes all started to increase earlier in pedicles than in pulp tissues (Luo *et al.*, 2013), indicating that softening in cherry fruit begins with pedicle dehydration, and that ABA plays a role in its regulation. Therefore, it can be assumed that the characteristics of stress resistance in fruit are related to its special morphological structure. Recent studies have shown that many genes respond to ABA in fruits under stress. For example, expression of *Fxaltp*, a strawberry gene encoding a non-specific lipid transfer protein, responds to ABA, wounding, and cold stress (Yubero-Serrano *et al.*, 2003). Using a Bulked Segregant Gene Expression Analysis (BSGA) approach, many new cold-regulated genes have been identified in peach, which provides the foundation for further experiments to explore the network of gene regulation in the cold and to determine the function of cold-responsive genes in peach fruits (Pons *et al.*, 2014). Recently, it has been reported that spraying the entire plant with ABA increases xylem sap flow and Ca^{2+} movement into the fruit, resulting in higher water-soluble apoplastic Ca^{2+} concentrations, reduced membrane leakage, and reduced fruit susceptibility to blossom-end rot development (Tonetto de Freitas *et al.*, 2014).

In addition, the ABA–glucose conjugation pathway also participates in the regulation of cellular ABA levels under conditions of stress (Iuchi *et al.*, 2001; Seo and Koshiba, 2002). In strawberry, *FaBG3* expression increases more rapidly than *FaNCED2* expression following dehydration treatment, which suggests that ABA produced by BGs occurs faster than through the lengthy and complex *de novo* biosynthesis pathways involving *FaNCED2*. It is possible that under conditions of abiotic stress, it is difficult for plants to increase endogenous ABA levels that result from *de novo* synthesis of proteins. This is supported by the observation that *FaBG3*-RNAi fruits exhibit down-regulated expression of dehydration-responsive proteins (FaRDs), calcineurin B-like protein (FaCBL), and dehydration responsive-element binding protein (FaDREB1B). The gene-silenced fruits also show a variety of ABA-deficient phenotypes, including failure to close the stomates fully on the sepals, and more rapid water loss in both sepals and fruits compared with the controls (Li *et al.*, 2013). Therefore, the ABA–glucose ester hydrolysis pathway is important, as these conjugates provide fruits with a means to increase ABA levels rapidly which enable them to respond to dehydration stress, despite the presence of intact *de novo* biosynthetic pathways. Fruits, like whole plants, are subjected to ever-changing environmental conditions, and, accordingly, they require constant fine-tuning of the active ABA pools to respond to the severity and duration of the stress. In future studies, it will be important to identify the site of action of the BGs, the specific reaction substrates, and the transporter of the BG enzymes in fruits under stress conditions.

Conclusions and future prospects

During fruit ripening, ABA accumulation appears to be critical, because it participates in the regulation of ripening of both climacteric and non-climacteric fruits, although the exact role of ABA remains obscure. Many basic scientific issues remain unclear, such as the mechanisms behind early expression of *NCED* genes that encode the key enzyme of ABA synthesis. In other words, how is the transcription of *NCED* induced at the onset of fruit ripening? The existence of different ABA sources, together with ABA transporters and multiple ABA receptors in different subcellular compartments, may allow fruits to have multiple ABA signalling circuits. This aspect raises an important question about how ABA production is coordinated in fruits as a whole. Plants must have a mechanism to coordinate these multiple ABA sources and signalling pathways as well as to regulate transport in order to achieve the desired cellular ABA levels under variable developmental stages and environmental conditions. A new strategy is needed to address these questions. In previous research into

fruit ripening, most of the studies focus on a single point (such as the role of ABA) or process (such as ABA metabolism and regulation); therefore, these research results are unable to explain the relationships between the biological processes in a highly complex three-dimensional network. We propose that future investigations need to take a systems biology approach when investigating the fruit-specific-ABA-deficient transcriptome, proteome, and metabolome. We should: (i) examine the roles of ABA in the regulation of fruit ripening in the context of gene signalling, metabolic networks, and key node point genes, as well as the control mechanisms during the onset of fruit ripening and subsequent processes; (ii) identify the response and downstream effects of key node point genes and signal molecules on artificial regulation; and (iii) establish the necessary technology for artificial regulation and control of key genes during the onset of fruit ripening and subsequent processes as a first step for breeding or post-harvest technology applications.

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References

Abeles FB, Morgan PW, Saltveit ME. 1992. *Ethylene in plant biology* . New York: Academic Press.

Alexander L, Grierson D. 2002. Ethylene biosynthesis and action in tomato: a model for climacteric fruit ripening. *Journal of Experimental Botany* **53,** 2039–2055.

Alvaro S, Ruiz KB, Ravaglia D, Costa G, Torrigiani P. 2013. ABA may promote or delay peach fruit ripening through modulation of ripening- and hormone-related gene expression depending on the developmental stage. *Plant Physiology and Biochemistry* **64,** 11–24.

Antoni R, Rodriguez L, Gonzalez-Guzman M, Pizzio GA, Rodriguez PL. 2011. News on ABA transport, protein degradation, and ABFs/WRKYs in ABA signaling. *Current Opinion in Plant Biology* **14,** 547–553.

Archbold DD, Dennis FG Jr. 1984. Quantification of free ABA and free and conjugated IAA in strawberry achene and receptacle tissue during fruit development. *Journal of the American Society for Horticultural Science* **109,** 330–335.

Ban T, Ishimaru M, Kobayashi S, Shiozaki S, Goto-Yamamoto N, Horiuchi S. 2003. Abscisic acid and 2,4-dichlorophenoxyacetic acid affect the expression of anthycyanin biosynthesic pathway genes in 'Kyoho' grape berries. *Journal of Horticultural Science and Biotechnology* **78,** 586–589.

Barry C. 2010. Factors influencing the ripening and quality of fleshy fruits. *Annual Plant Reviews* **38,** 296–326.

Berli FJ, Fanzone M, Piccoli P, Bottini R. 2011. Solar UV-B and ABA are involved in phenol metabolism of Vitis vinifera L. Increasing biosynthesis of berry skin polyphenols. *Journal of Agricultural and Food Chemistry* **59,** 4874–4884.

Bino RJ, Ric de Vos CH, Lieberman M, Hall RD, Bovy A, Jonker HH, Tikunov Y, Lommen A, Moco S, Levin I. 2005. The light-hyperresponsive *high pigment-2dg* mutation of tomato: alterations in the fruit metabolome. *New Phytologist* **166,** 427–438.

Bleecker AB, Kende H. 2000. Ethylene: a gaseous signal molecule in plants. *Annual Review of Cell and Developmental Biology* **16,** 1–18.

Boursiac Y, Leran S, Corratge-Faillie C, Gojon A, Krouk G, Lacombe B. 2013. ABA transport and transporters. *Trends in Plant Science* **18,** 325–333.

Brummell DA, Harpster MH, Dunsmuir P. 1999. Differential expression of expansin gene family members during growth and ripening of tomato fruit. *Plant Molecular Biology* **39,** 161–169.

Brzobohaty B, Moore I, Kristoffersen P, Bako L, Campos N, Schell J, Palme K. 1993. Release of active cytokinin by a beta-glucosidase localized to the maize root meristem. *Science* **262,** 1051–1054.

Buesa C, Dominguez M, Vendrell M. 1994. Abscisic acid effects on ethylene production and respiration rate in detached apple fruits at different stages of development. *Revista Espanola de Cienciay y Tecnologia de Alimentos* **34,** 495–506.

Burbidge A, Grieve TM, Jackson A, Thompson A, McCarty DR, Taylor IB. 1999. Characterization of the ABA-deficient tomato mutant *notabilis* and its relationship with maize *Vp14*. *The Plant Journal* **17,** 427–431.

Burla B, Pfrunder S, Nagy R, Francisco RM, Lee Y, Martinoia E. 2013. Vacuolar transport of abscisic acid glucosyl ester is mediated by ATP-binding cassette and proton-antiport mechanisms in Arabidopsis. *Plant Physiology* **163,** 1446–1458.

Cakir B, Agasse A, Gaillard C, Saumonneau A, Delrot S, Atanassova R. 2003. A grape ASR protein involved in sugar and abscisic acid signaling. *The Plant Cell* **15,** 2165–2180.

Carpita NC, Gibeaut DM. 1993. Structural models of primary cell walls in flowering plants: consistency of molecular structure with the physical properties of the walls during growth. *The Plant Journal* **3,** 1–30.

Cheng WH, Endo A, Zhou L, *et al*. 2002. A unique short-chain dehydrogenase/reductase in Arabidopsis glucose signalling and abscisic acid biosynthesis and functions. *The Plant Cell* **14,** 2723–2743.

Chernys JT, Zeevaart JAD. 2000. Characterization of the 9-*cis*-epoxycarotenoid dioxygenase gene family and the regulation of abscisic acid biosynthesis in avocado. *Plant Physiology* **124,** 343–354.

Choi H, Hong J, Ha J, Kang J, Kim SY. 2000. ABFs, a family of ABA responsive element binding factors. *Journal of Biological Chemistry* **275,** 1723–1730.

Chung MY, Vrebalov J, Alba R, Lee J, McQuinn R, Chung JD, Klein P, Giovannoni J. 2010. A tomato (*Solanum lycopersicum*) *APETALA2/ERF* gene, *SlAP2a*, is a negative regulator of fruit ripening. *The Plant Journal* **64,** 936–947.

Cosgrove DJ. 2000. Expansive growth of plant cell walls. *Plant Physiology and Biochemistry* **38,** 109–124.

Dekkers BJW, Schuurmans JAMJ, Smeekens SCM. 2004. Glucose delays seed germination in *Arabidopsis thaliana*. *Planta* **218,** 579–588.

DellaPenna D, Pogson BJ. 2006. Vitamin synthesis in plants: tocopherols and carotenoids. *Annual Review of Plant Biology* **57,** 711–738.

Deluc LG, Grimplet J, Wheatley MD, Tillett RL, Quilici DR, Osborne C, Schooley DA, Schlauch KA, Cushman JC, Cramer GR. 2007. Transcriptomic and metabolite analyses of Cabernet Sauvignon grape berry development. *BMC Genomics* **8,** 429.

Deluc LG, Quilici DR, Decendit A, Grimplet J, Wheatley MD, Schlauch KA, Merillon JM, Cushman JC, Cramer GR. 2009. Water deficit alters differentially metabolic pathways affecting important flavor and quality traits in grape berries of Cabernet Sauvignon and Chardonnay. *BMC Genomics* **10,** 212.

Deytieux C, Geny L, Lapaillerie D, Claverol S, Bonneu M, Doneche B. 2007. Proteome analysis of grape skins during ripening. *Journal Experimental Botany* **58,** 1851–1862.

Eccher G, Ferrerob S, Populina F, Colombob L, Botton A. 2014. Apple (*Malus domestica* L. Borkh) as an emerging model for fruit development. *Plant Biosystems* **148, doi.** org/10.1080/11263504.2013.870254

Else MA, Stankiewicz-Davies AP, Crisp CM, Atkinson CJ. 2004. The role of polar auxin transport through pedicels of *Prunus avium* L. in relation to fruit development and retention. *Journal of Experimental Botany* **55,** 2099–2109.

Endo A, Sawada Y, Takahashi H, *et al*. 2008. Drought induction of Arabidopsis 9-*cis*-epoxycarotenoid dioxygenase occurs in vascular parenchyma cells. *Plant Physiology* **147,** 1984–1993.

Estevez JM, Cantero A, Reindl A, Reichler S, Leon P. 2001. 1-Deoxy-D-xylulose-5-phosphate synthase, a limiting enzyme for plastidic isoprenoid biosynthesis in plants. *Journal of Biological Chemistry* **276,** 22901–22909.

Feng YM, Wei XK, Liao WX, Huang LH, Zhang H, Liang SC, Peng H. 2013. Molecular analysis of the annexin gene family in soybean. *Biologia Plantarum* **57,** 655–662.

Finkelstein RR, Gibson SI. 2001. ABA and sugar interactions regulating development: cross-talk or voices in a crowd? *Current Opinion in Plant Biology* **5,** 26–32.

Fraser PD, Romer S, Shipton CA, Mills PB, Kiano JW, Misawa N, Drake RG, Schuch W, Bramley PM. 2002. Evaluation of transgenic tomato plants expression an additional phytoene synthase in a fruit-specific manner. *Proceedings of the National Academy of Sciences, USA* **99,** 1092–1097.

Frey A, Audran C, Marin E, Sotta B, Marion-Poll A. 1999. Engineering seed dormancy by the modification of zeaxanthin epoxidase gene expression. *Plant Molecular Biology* **39,** 1267–1274.

Fujita Y, Nakashima K, Yoshida T, *et al*. 2009. Three SnRK2 protein kinases are the main positive regulators of abscisic acid signaling in response to water stress in Arabidopsis. *Plant and Cell Physiology* **50,** 2123–2132.

Galpaz N, Wang Q, Menda N, Zamir D, Hirschberg J. 2008. Abscisic acid deficiency in the tomato mutant *high-pigment 3* leading to increased plastid number and higher fruit lycopene content. *The Plant Journal* **53,** 717–730.

Gambetta GA, Matthews MA, Shaghasi TH, McElrone AJ, Castellarin SD. 2010. Sugar and abscisic acid signaling orthologs are activated at the onset of ripening in grape. *Planta* **232,** 219–234.

Gazzarrini S, McCourt P. 2001. Genetic interactions between ABA, ethylene and sugar signaling pathways. *Current Opinion in Plant Biology* **4,** 387–391.

Giovannoni J. 2001. Molecular biology of fruit maturation and ripening. *Annual Review of Plant Physiology and Plant Molecular Biology* **52,** 725–749.

Giovannoni JJ. 2004. Genetic regulation of fruit development and ripening. *The Plant Cell* **16,** S170–S180.

Giovannoni JJ. 2007. Fruit ripening mutants yield insights into ripening control. *Current Opinion in Plant Biology* **10,** 283–289.

Giribaldi M, Gény L, Delrot S, Schubert A. 2010. Proteomic analysis of the effects of ABA treatments on ripening *Vitis vinifera* berries. *Journal of Experimental Botany* **61,** 2447–2458.

Gómez-Porras JL, Riaño-Pachón DM, Dreyer I, Mayer JE, Mueller-Roeber B. 2007. Genome-wide analysis of ABA-responsive elements ABRE and CE3 reveals divergent patterns in Arabidopsis and rice. *BMC Genomics* **8,** 260–273.

Gonzalez-Ballester D, Pollock SV, Pootakham W, Grossman AR. 2008. The central role of a SNRK2 kinase in sulfur deprivation responses. *Plant Physiology* **147,** 216–227.

Gonzalez-Guzman M, Pizzio GA, Antoni R *et al.* 2012. *Arabidopsis* PYR/PYL/RCAR receptors play a major role in quantitative regulation of stomatal aperture and transcriptional response to abscisic acid. *The Plant Cell* **24,** 2483–2496.

Hartung W, Sauter A, Hose E. 2002. Abscisic acid in the xylem: where does it come from, where does it go to? *Journal of Experimental Botany* **53,** 27–32.

Hattori T, Totsuka M, Hobo T, Kagaya Y, Yamamoto-Toyoda A. 2002. Experimentally determined sequence requirement of ACGT-containing abscisic acid response element. *Plant and Cell Physiology* **43,** 136–140.

Hiwasa K, Kinugasa Y, Amano S, Hashimoto A, Nakano R, Inaba A, Kubo Y. 2003. Ethylene is required for both the initiation and progression of softening in pear (*Pyrus communis* L.) fruit. *Journal of Experimental Botany* **54,** 771–779.

Huber DJ. 1983. Polyuronide degradation and hemicellulose modification in ripening tomato fruit. *Journal of the American Society for Horticultural Science* **108,** 405–409.

Huo H, Dahal P, Kunusoth K, McCallum CM, Bradford KJ. 2013. Expression of 9-cis-EPOXYCAROTENOID DIOXYGENASE4 is essential for thermoinhibition of lettuce seed germination but not for seed development or stress tolerance. *The Plant Cell* **25,** 884–900.

Itkin M, Seybold H, Breitel D, Rogachev I, Meir S, Aharoni A. 2009. TOMATO AGAMOUS-LIKE 1 is a component of the fruit ripening regulatory network. *The Plant Journal* **60,** 1081–1095.

Iuchi S, Kobayashi M, Taji T, Naramoto M, Seki M, Kato T, Tabata S, Kakubari Y, Yamaguchi-Shinozaki K, Shinozaki K. 2001. Regulation of drought tolerance by gene manipulation of 9-*cis*-epoxycarotenoid dioxygenase, a key enzyme in abscisic acid biosynthesis in *Arabidopsis*. *The Plant Journal* **27,** 325–333.

Jaakola L, Poole M, Jones MO, *et al*. 2010. A SQUAMOSA MADS box gene involved in the regulation of anthocyanin accumulation in bilberry fruits. *Plant Physiology* **153,** 1619–1629.

Jeong ST, Goto-Yamamoto N, Kobayashi S, Esaka M. 2004. Effects of plant hormones and shading on the accumulation of anthocyanins and the expression of anthocyanin biosynthetic genes in grape berry skins. *Plant Science* **167,** 247–252.

Ji K, Chen P, Sun L, *et al*. 2012. Non-climacteric ripening in strawberry fruit is linked to ABA, *FaNCED2* and *FaCYP707A1. Functional Plant Biology* **39,** 351–357.

Jia HF, Chai YM, Li CL, Lu D, Luo JJ, Qin L, Shen YY. 2011. Abscisic acid plays an important role in the regulation of strawberry fruit ripening. *Plant Physiology* **157,** 188–199.

Jia HF, Wang YH, Sun MZ, *et al*. 2013. Sucrose functions as a signal involved in the regulation of strawberry fruit development and ripening. *New Phytologist* **198,** 453–465.

Jiang F, Hartung W. 2008. Long-distance signaling of abscisic acid (ABA): the factors regulating the intensity of the ABA signal. *Journal of Experimental Botany* **59,** 37–43.

Kachanovsky DE, Filler S, Isaacson T, Hirschberg J. 2012. Epistasis in tomato color mutations involves regulation of *phytoene synthase 1* expression by *cis*-carotenoids. *Proceedings of the National Academy of Sciences, USA* **109,** 19021–19026.

Kang JY, Choi HI, Im MY, Kim SY. 2002. Arabidopsis basic leucine zipper proteins that mediate stress-responsive abscisic acid signaling. *The Plant Cell* **14,** 343–357.

Karlova R, Rosin FM, Busscher-Lange J, Parapunova V, Do PT, Fernie AR, Fraser PD, Baxter C, Angenent GC, de Maagd RA. 2011. Transcriptome and metabolite profiling show that APETALA2a is a major regulator of tomato fruit ripening. *The Plant Cell* **23,** 923–941.

Karppinen K, Hirvelä E, Nevala T, Sipari N, Suokas M, Jaakola L. 2013. Changes in the abscisic acid levels and related gene expression during fruit development and ripening in bilberry (*Vaccinium myrtillus* L.). *Phytochemistry* **95,** 127–134.

Klee HJ, Giovannoni JJ. 2011. Genetics and control of tomato fruit ripening and quality attributes. *Annual Review of Genetics* **45,** 41–59.

Klingler JP, Batelli G, Zhu JK. 2010. ABA receptors: the START of a new paradigm in phytohormone signalling. *Journal of Experimental Botany* **61,** 3199–3210.

Kojima K, Yamada Y, Yamamoto M. 1995. Effects of abscisic acid injection on sugar and organic acid contents of citrus fruit. *Japanese Society for Horticultural Science* **64,** 17–21.

Koiwai H, Nakaminami K, Seo M, Mitsuhashi W, Toyomasu T, Koshiba T. 2004. Tissue-specific localization of an abscisic acid biosynthetic enzyme, AAO3, in Arabidopsis. *Plant Physiology* **134,** 1697–1707.

Kolotilin I, Koltai H, Tadmor Y, Bar-Or C, Reuveni M, Meir A, Nahon S, Shlomo H, Chen L, Levin I. 2007. Transcriptional profiling of *high pigment-2dg* tomato mutant links early fruit plastid biogenesis with its overproduction of phytonutrients. *Plant Physiology* **145,** 389–401.

Kondo S, Inoue K. 1997. Abscisic acid (ABA) and 1-aminocyclopropane-1-carboxylic acid (ACC) content during growth of 'Satonishiki' cherry fruit, and the effect of ABA and ethephon application on fruit quality. *Journal of Horticultural Science* **72,** 221–227.

Koyama K, Sadamatsu K, Goto-Yamamoto N. 2010. Abscisic acid stimulated ripening and gene expression in berry skins of the Cabernet Sauvignon grape. *Functional and Integrative Genomics* **10,** 367–381.

Kushiro T, Okamoto M, Nakabayashi K, Yamagishi K, Kitamura S, Asami T, Hirai N, Koshiba T, Kamiya Y, Nambara E. 2004. The *Arabidopsis* cytochrome P450 CYP707A encodes ABA 8'-hydroxylases: key enzymes in ABA catabolism. *The EMBO Journal* **23,** 1647–1656.

Lacampagne S, Gagne S, Geny L. 2009. Involvement of abscisic acid in controlling the proanthocyanidin biosynthesis pathway in grape skin: new elements regarding the regulation of tannin composition and leucoanthocyanidin reductase (LAR) and anthocyanidin reductase (ANR) activities and expression. *Journal of Plant Growth Regulation* **29,** 81–90.

Lara I, Vendrell M. 2000. Changes in abscisic acid levels, ethylene biosynthesis, and protein patterns during fruit maturation of 'Granny Smith' apples. *Journal of the American Society for Horticultural Science* **125,** 183–189.

Lashbrook CC, Gonzalez-Bosch C, Bennett AB. 1994. Two divergent endo-beta-1,4-glucanase genes exhibit overlapping expression in ripening fruit and abscising flowers. *The Plant Cell* **6,** 1485–1493.

Lee JM, Joung JG, McQuinn R, Chung MY, Fei ZJ, Tieman D, Klee H, Giovannoni J. 2012. Combined transcriptome, genetic diversity and metabolite profiling in tomato fruit reveals that the ethylene response factor *SlERF6* plays an important role in ripening and carotenoid accumulation. *The Plant Journal* **70,** 191–204.

Lee KH, Piao HL, Kim HY, Choi SM, Jiang F, Hartung W, Hwang I, Kwak JM, Lee IJ, Hwang I. 2006. Activation of glucosidase via stress-induced polymerization rapidly increases active pools of abscisic acid. *Cell* **126,** 1109–1120.

Leng P, Zhang GL, Li XX, Wang LH, Zheng ZM. 2009. Cloning of 9-*cis*-epoxycarotenoid dioxygenase (NCED) gene encoding a key enzyme during abscisic acid (ABA) biosynthesis and ABA-regulated ethylene production in detached young calyx. *Chinese Science Bulletin* **54,** 2830–2838.

Li Q, Ji K, Sun YF, Luo H, Wang HQ, Leng P. 2013. The role of *FaBG3* in fruit ripening and *B. cinerea* fungal infection of strawberry. *The Plant Journal* **76,** 24–35.

Lindgren LO, Stalberg KG, Hoglund AS. 2003. Seed-specific overexpression of an endogenous Arabidopsis phytoene synthase gene results in delayed germination and increased levels of carotenoids, chlorophyll, and abscisic acid. *Plant Physiology* **132,** 968–981.

Liu XD, Zhang H, Zhao Y, Feng ZY, Li Q, Yang HQ, Luan S, Li JM, He ZH. 2013. Auxin controls seed dormancy through stimulation of abscisic acid signaling by inducing ARF-mediated *ABI3* activation in *Arabidopsis*. *Proceedings of the National Academy of Sciences, USA* **110,** 15485–15490.

Liu XG, Yue YL, Li B, Nie YL, Li W, Wu WH, Ma LG. 2007. A G protein-coupled receptor is a plasma membrane receptor for the plant hormone abscisic acid. *Science* **315,** 1712–1716.

Lovisetto A, Guzzo F, Tadiello A, Confortin E, Pavanello A, Botton A, Casadoro G. 2013. Characterization of a bZIP gene highly expressed during ripening of the peach fruit. *Plant Physiology and Biochemistry* **70,** 462–470

Luo H, Dai SJ, Ren J, *et al*. 2013. The role of ABA in the maturation and postharvest life of a nonclimacteric sweet cherry fruit. *Journal of Plant Growth Regulation* doi: 10.1007/s00344-013-9388-7.

Ma Y, Szostkiewicz I, Korte A, Moes D, Yang Y, Christmann A, Grill E. 2009. Regulators of PP2C phosphatase activity function as abscisic acid sensors. *Science* **324,** 1064–1068.

Manning K, Tör M, Poole M, Hong YG, Thompson AJ, King GJ, Giovannoni JJ, Seymour GB. 2006. A naturally occurring epigenetic mutation in a gene encoding an SBP-box transcription factor inhibits tomato fruit ripening. *Nature Genetics* **38,** 948–952.

Martel C, Vrebalov J, Tafelmeyer P, Giovannoni JJ. 2011. The tomato MADS-box transcription factor RIPENING INHIBITOR interacts with promoters involved in numerous ripening processes in a COLORLESS NONRIPENING-dependent manner. *Plant Physiology* **157,** 1568–1579.

Matas AJ, Yeats TH, Buda GJ, *et al*. 2011. Tissue- and cell-type specific transcriptome profiling of expanding tomato fruit provides insights into metabolic and regulatory specialization and cuticle formation. *The Plant Cell* **23,** 3893–3910.

Medina-Puche L, Cumplido-Laso G, Amil-Ruiz F, Hoffmann T, Ring L, Rodríguez-Franco A, Caballero JL, Schwab W, Muñoz-Blanco J, Blanco-Portales R. 2013. *MYB10* plays a major role in the regulation of flavonoid/phenylpropanoid metabolism during ripening of *Fragaria ×ananassa* fruits. *Journal of Experimental Botany* **65,** 401–417.

Melcher K, Ng LM, Zhou XE, *et al*. 2009. A gate–latch–lock mechanism for hormone signalling by abscisic acid receptors. *Nature* **462,** 602–608.

Mittelheuser CJ, van Steveninck RFM. 1969. Stomatal closure and inhibition of transpiration induced by (RS)-abscisic acid. *Nature* **221,** 281–282.

Mochizuki N, Brusslan JA, Larkin R, Nagatani A, Chory J. 2001. Arabidopsis genomes uncoupled 5 (GUN5) mutant reveals the involvement of Mg-chelatase H subunit in plastid-to-nucleus signal transduction. *Proceedings of the National Academy of Sciences, USA* **98,** 2053–2058.

Muller AH, Hansson M. 2009. The barley magnesium chelatase 150-kD subunit is not an abscisic acid receptor. *Plant Physiology* **150,** 157–166.

Nakano R, Ogura E, Kubo Y, Inaba A. 2003. Ethylene biosynthesis in detached young persimmon fruit is initiated in calyx and modulated by water loss from the fruit. *Plant Physiology* **131,** 276–286.

Nicolas P, Lecourieux D, Kappel C, Cluzet S, Cramer G, Delrot S, Lecourieux F. 2014. The basic leucine zipper transcription factor ABSCISIC ACID RESPONSE ELEMENT-BINDING FACTOR2 is an important transcriptional regulator of abscisic acid-dependent grape berry ripening processes. *Plant Physiology* **164,** 365–383.

Nijhawan A, Jain M, Tyagi AK, Khurana JP. 2008. Genomic survey and gene expression analysis of the basic leucine zipper transcription factor family in rice. *Plant Physiology* **146,** 333–350.

Nishimura N, Hitomi K, Arvai AS, Rambo RP, Hitomi C, Cutler SR, Schroeder JI, Getzoff ED. 2009. Structural mechanism of abscisic acid binding and signaling by dimeric PYR1. *Science* **326,** 1373–1379.

Nishiyama K, Guis M, Rose JKC, *et al*. 2007. Ethylene regulation of fruit softening and cell wall disassembly in Charentais melon. *Journal of Experimental Botany* **58,** 1281–1290.

Nitsch LMC, Oplaat C, Feron R, Ma Q, Wolters-Arts M, Hedden P, Mariani C, Vriezen WH. 2009. Abscisic acid levels in tomato ovaries are regulated by *LeNCED1* and *SlCYP707A1*. *Planta* **229**. 1335–1346.

North HM, De Almeida A, Boutin JP, Frey A, To A, Botran L, Sotta B, Marion-Poll A. 2007. The Arabidopsis ABA-deficient mutant *aba4* demonstrates that the major route for stress-induced ABA accumulation is via neoxanthin isomers. *The Plant Journal* **50,** 810–824.

Pandy S, Nelson DC, Assmann SM. 2009. Two novel GPCR-type G proteins are abscisic acid receptors in *Arabidopsis*. *Cell* **136,** 136–148.

Park SY, Fung P, Nishimura N, *et al*. 2009. Abscisic acid inhibits type 2C protein phosphatases via the PYR/PYL family of START proteins. *Science* **324,** 1068–1071.

Pons C, Martí C, Forment J, Crisosto CH, Dandekar AM, Granell A. 2014. A bulk segregant gene expression analysis of a peach population reveals components of the underlying mechanism of the fruit cold response. *PLoS One* **9,** e90706.

Price J, Li TC, Kang SG, Na JK, Jang JC. 2003. Mechanisms of glucose signaling during germination of Arabidopsis. *Plant Physiology* **132,** 1424–1438.

Qin XQ, Zeevaart JAD. 1999. The 9-*cis*-epoxycarotenoid cleavage reaction is the key regulatory step of abscisic acid biosynthesis in water-stressed bean. *Proceedings of the National Academy of Sciences, USA* **96,** 15354–15361.

Qin XQ, Zeevaart JAD. 2002. Overexpression of a 9-*cis*-epoxycarotenoid dioxygenase gene in *Nicotiana plumbaginifolia* increases abscisic acid and phaseic acid levels and enhances drought tolerance. *Plant Physiology* **128,** 544–551.

Ren J, Chen P, Dai SJ, Li P, Li Q, Ji K, Wang YP, Leng P. 2011. Role of abscisic acid and ethylene in sweet cherry fruit maturation: molecular aspects. *New Zealand Journal of Crop and Horticultural Science* **39,** 1–14.

Ren J, Sun L, Wu JF, Zhao SL, Wang CL, Wang YP, Ji K, Leng P. 2010. Cloning and expression analysis of cDNAs for ABA 8′-hydroxylase during sweet cherry fruit maturation and under stress conditions. *Journal of Plant Physiology* **167,** 1486–1493.

Rodrigo MJ, Alquezar B, Zacarias L. 2006. Cloning and characterization of two 9-*cis*-epoxycarotenoid dioxygenase genes, differentially regulated during fruit maturation and under stress conditions, from orange (*Citrus sinensis* L. Osbeck). *Journal of Experimental Botany* **57,** 633–643.

Rodrigo MJ, Marcos JF, Alferez F, Mallent MD, Zacarias L. 2003. Characterization of Pinalate, a novel *Citrus sinensis* mutant with a fruit-specific alteration that results in yellow pigmentation and decreased ABA content. *Journal of Experimental Botany* **54,** 727–738.

Rolland F, Baeno-Gonzalez E, Sheen J. 2006. Sugar sensing and signaling in plants: conserved and novel mechanisms. *Annual Review of Plant Biology* **57,** 675–709.

Romero P, Lafuente MT, Rodrigo MJ. 2012. The *Citrus* ABA signalosome: identification and transcriptional regulation during sweet orange fruit ripening and leaf dehydration. *Journal of Experimental Botany* **63,** 4931–4945.

Saito S, Hirai N, Matsumoto C, Ohigashi H, Ohta D, Sakata K, Mizutani M. 2004. Arabidopsis *CYP707A*s encode (+)-abscisic acid

8'-hydroxylase, a key enzyme in the oxidative catabolism of abscisic acid. *Plant Physiology* **134,** 1439–1449.

Saladie M, Matas AJ, Isaacson T, *et al*. 2007. A reevaluation of the key factors that influence tomato fruit softening and integrity. *Plant Physiology* **144,** 1012–1028.

Santiago J, Dupeux F, Round A, Antoni R, Park SY, Jamin M, Cutler SR, Rodriguez PL, Marquez JA. 2009. The abscisic acid receptor PYR1 in complex with abscisic acid. *Nature* **462,** 665–668.

Sauter A, Dietz KJ, Hartung W. 2002. A possible stress physiological role of abscisic acid conjugates in root-to-shoot signaling. *Plant, Cell and Environment* **25,** 223–228.

Schwartz SH, Qin XQ, Zeevaart JAD. 2003. Elucidation of the indirect pathway of abscisic acid biosynthesis by mutants, genes, and enzymes. *Plant Physiology* **131,** 1591–1601.

Schweighofer A, Hirt H, Meskiene I. 2004. Plant PP2C phosphatases: emerging functions in stress signaling. *Trends in Plant Science* **9,** 236–243.

Seo M, Koshiba T. 2002. Complex regulation of ABA biosynthesis in plants. *Trends in Plant Science* **7,** 41–48.

Seo M, Koshiba T. 2011. Transport of ABA from the site of biosynthesis to the site of action. *Journal of Plant Research* **124,** 501–507.

Seki M, Umezawa T, Urano K, Shinozaki K. 2007. Regulatory metabolic networks in drought stress responses. *Current Opinion in Plant Biology* **10,** 296–302.

Setha S, Kondo S, Hirai N, Ohigashi H. 2005. Quantification of ABA and its metabolites in sweet cherries using deuterium-labeled internal standards. *Plant Growth Regulation* **45,** 183–188.

Seymour GB, Chapman NH, Chew BL, Rose JKC. 2013*a*. Regulation of ripening and opportunities for control in tomato and other fruits. *Plant Biotechnology Journal* **11,** 269–278.

Seymour GB, Ostergaard L, Chapman NH, Knapp S, Martin C. 2013*b*. Fruit development and ripening. *Annual Review of Plant Biology* **64,** 219–241.

Seymour G, Poole M, Manning K, King GJ. 2008. Genetics and epigenetics of fruit development and ripening. *Current Opinion in Plant Biology* **11**. 58–63.

Shang Y, Yan L, Liu ZQ, *et al*. 2010. The Mg-chelatase H subunit of *Arabidopsis* antagonizes a group of WRKY transcription repressors to relieve ABA-responsive genes of inhibition. *The Plant Cell* **22,** 1909–1935.

Shen XJ, Zhao K, Liu LL, Zhang KC, Huazhao Yuan HZ, Liao X, Wang Q, Xinwei Guo XW, Li F, Li TH. 2014. A role for PacMYBA in ABA-regulated anthocyanin biosynthesis in red-colored sweet cherry cv. Hong Deng (*Prunus avium* L.). *Plant and Cell Physiology* (in press).

Shen YY, Wang XF, Wu FQ, *et al*. 2006. The Mg-chelatase H subunit is an abscisic acid receptor. *Nature* **443,** 823–826.

Smeekens S. 2000. Sugar-induced signal transduction in plants. *Annual Review of Plant Physiology and Plant Molecular Biology* **51,** 49–81.

Smith DL, Gross KC. 2000. A family of at least seven β-galactosidase genes is expressed during tomato fruit development. *Plant Physiology* **123,** 1173–1184.

Srivastava A, Handa AK. 2005. Hormonal regulation of tomato fruit development: a molecular perspective. *Journal of Plant Growth Regulation* **24,** 67–82.

Sun L, Sun YF, Zhang M, *et al*. 2012*a*. Suppression of 9-*cis*-epoxycarotenoid dioxygenase, which encodes a key enzyme in abscisic acid biosynthesis, alters fruit texture in transgenic tomatoes. *Plant Physiology* **158,** 283–298.

Sun L, Wang YP, Chen P, Ren J, Ji K, Li Q, Li P, Dai SJ, Leng P. 2011. Transcriptional regulation of *SlPYL*, *SlPP2C* and *SlSnRK2* gene families encoding ABA signal core components during tomato fruit development and drought stress. *Journal of Experimental Botany* **62,** 5659–5669.

Sun L, Yuan B, Zhang M, Wang L, Cui MM, Wang Q, Leng P. 2012*b*. Fruit-specific RNAi-mediated suppression of *SlNCED1* increases both lycopene and β-carotene contents in tomato fruit. *Journal of Experimental Botany* **63,** 3097–3108.

Sun L, Zhang M, Ren J, Qi JX, Zhang GJ, Leng P. 2010. Reciprocity between abscisic acid and ethylene at the onset of berry ripening and after harvest. *BMC Plant Biology* **10,** 257.

Sun YF, Chen P, Duan CR, *et al.* 2013. Transcriptional regulation of genes encoding key enzymes of abscisic acid metabolism during melon (*Cucumis melo* L.) fruit development and ripening. *Journal of Plant Growth Regulation* **32,** 233–244.

Takata M. 1983. Respiration, ethylene production and ripening of Japanese persimmon fruit harvested at various stages of development. *Journal of the Japanese Society for Horticultural Science* **52,** 78–84.

Tan BC, Cline K, McCarty DR. 2001. Localization and targeting of the VP14 epoxy-carotenoid dioxygenase to chloroplast membranes. *The Plant Journal* **27,** 373–382.

Tan BC, Schwartz SH, Zeevaart JAD, McCarty DR. 1997. Genetic control of abscisic acid biosynthesis in maize. *Proceedings of the National Academy of Sciences, USA* **94,** 12235–12240.

Taylor IB, Burbidge A, Thompson AJ. 2000. Control of abscisic acid synthesis. *Journal of Experimental Botany* **51,** 1563–1574.

Taylor IB, Sonneveld T, Bugg TDH, Thompson AJ. 2005. Regulation and manipulation of the biosynthesis of abscisic acid, including the supply of xanthophyll precursors. *Journal of Plant Growth Regulation* **24,** 253–273.

Thompson AJ, Jackson AC, Symonds RC, Mulholland BJ, Dadswell AR, Blake PS, Burbidge A, Taylor IB. 2000. Ectopic expression of a tomato 9-*cis*-epoxycarotenoid dioxygenase gene causes over-production of abscisic acid. *The Plant Journal* **23,** 363–374.

Tieman DM, Harriman RW, Ramamohan G, Handa AK. 1992. An antisense pectin methylesterase gene alters pectin chemistry and soluble solids in tomato fruit. *The Plant Cell* **4,** 667–679.

Tigchelaar EC, Mcglasson WB, Franklin MJ. 1978. Natural and ethephon-stimulated ripening of F_1 hybrids of the ripening inhibitor (*rin*) and non-ripening (*nor*) mutants of tomato (*Lycopersicon esculentum* Mill.). *Australian Journal of Plant Physiology* **5,** 449–456.

Tikunov YM, Molthoff J, de Vos RCH, *et al*. 2013. NON-SMOKY GLYCOSYLTRANSFERASE1 prevents the release of smoky aroma from tomato fruit. *The Plant Cell* **25,** 3067–3078.

Tonetto de Freitas S, McElrone AJ, Shackel KA, Mitcham EJ. 2014. Calcium partitioning and allocation and blossom-end rot development in tomato plants in response to whole-plant and fruit-specific abscisic acid treatments. *Journal of Experimental Botany* **65,** 235–247.

Trainotti L, Pavanello A, Casadoro G. 2005. Different ethylene receptors show an increased expression during the ripening of strawberries: does such an increment imply a role for ethylene in the ripening of these non-climacteric fruits? *Journal of Experimental Botany* **56,** 2037–2046.

Tung SA, Smeeton R, White C, Black CR, Taylor IB, Hilton HW, Thompson AJ. 2008. Over-expression of *LeNCED1* in tomato (*Solanum lycopersicum* L.) with the *rbcS3C* promoter allows recovery of lines that accumulate very high levels of abscisic acid and exhibit severe phenotypes. *Plant, Cell and Environment* **31,** 968–981.

Umezawa T, Okamoto M, Kushiro T, Nambara E, Oono Y, Seki M, Kobayashi M, Koshiba T, Kamiya Y, Shinozaki K. 2006. CYP707A3, a major ABA 8'-hydroxylase involved in dehydration and rehydration response in *Arabidopsis thaliana*. *The Plant Journal* **46,** 171–182.

Vrebalov J, Ruezinsky D, Padmanabhan V, White R, Medrano D, Drake R, Schuch W, Giovannoni J. 2002. A MADS-box gene necessary for fruit ripening at the tomato *ripening-inhibitor* (*rin*) locus. *Science* **296,** 343–346.

Wang YP, Wang Y, Ji K, *et al*. 2013. The role of abscisic acid in regulating cucumber fruit development and ripening and its transcriptional regulation. *Plant Physiology and Biochemistry* **64,** 70–79.

Wang YP, Wu Y, Duan CR, *et al*. 2012. The expression profiling of the *CsPYL*, *CsPP2C* and *CsSnRK2* gene families during fruit development and drought stress in cucumber. *Journal of Plant Physiology* **169,** 1874–1882.

Wheeler S, Loveys B, Ford C, Davies C. 2009. The relationship between the expression of abscisic acid biosynthesis genes, accumulation of abscisic acid and the promotion of *Vitis vinifera* L. berry ripening by abscisic acid. *Australian Journal of Grape and Wine Research* **15,** 195–204.

White PJ. 2002. Recent advances in fruit development and ripening: an overview. *Journal of Experimental Botany* **53,** 1995–2000.

Wright STC, Hiron RWP. 1969. (+)-Abscisic acid, the growth inhibitor induced in detached wheat leaves by a period of wilting. *Nature* **224,** 719–720.

Wu FQ, Xin Q, Cao Z, *et al*. 2009. The magnesium-chelatase H subunit binds abscisic acid and functions in abscisic acid signaling: new evidence in Arabidopsis. *Plant Physiology* **150,** 1940–1954.

Xu ZY, Lee KH, Dong T, *et al*. 2012. A vacuolar β-glucosidase homolog that possesses glucose-conjugated abscisic acid hydrolyzing activity plays an important role in osmotic stress responses in *Arabidopsis*. *The Plant Cell* **24,** 2184–2199.

Yamaki S, Asakura T. 1991. Stimulation of the uptake of sorbitol into vacuoles from apple fruit flesh by abscisic acid and into protoplasts by indoleacetic acid. *Plant and Cell Physiology* **32,** 315–318.

Yen HC, Shelton BA, Howard LR, Lee S, Vrebalov J, Giovannoni JJ. 1997. The tomato high-pigment (hp) locus maps to chromosome 2 and influences plastome copy number and fruit quality. *Theoretical and Applied Genetics* **95,** 1069–1079.

Yin P, Fan H, Hao Q, Yuan XQ, Wu D, Pang YX, Yan CY, Li WQ, Wang JW, Yan N. 2009. Structural insights into the mechanism of abscisic acid signaling by PYL proteins. *Nature Structural and Molecular Biology* **16,** 1230–1236.

Yoshida T, Fujita Y, Sayama H, Kidokoro S, Maruyama K, Mizoi J, Shinozaki K, Yamaguchi-Shinozaki K. 2010. AREB1, AREB2, and ABF3 are master transcription factors that cooperatively regulate ABRE-dependent ABA signaling involved in drought stress tolerance and require ABA for full activation. *The Plant Journal* **61,** 672–685.

Yubero-Serrano EM, Moyano E, Medina-Escobar N, oz-Blanco JM, Caballero JA. 2003. Identication of a strawberry gene encoding a non-specic lipid transfer protein that responds to ABA, wounding and cold stress. *Journal of Experimental Botany* **54,** 1865–1877.

Zaharah SS, Singh Z, Symons GM, Reid JB. 2013. Mode of action of abscisic acid in triggering ethylene biosynthesis and softening during ripening in mango fruit. *Postharvest Biology and Technology* **75,** 37–44.

Zhang GJ, Duan CR, Wang Y, *et al*. 2013. The expression pattern of b-glucosidase genes (VvBGs) during grape berry maturation and dehydration stress. *Plant Growth Regulation* **70,** 105–114.

Zhang M, Leng P, Zhang GL, Li XX. 2009*b*. Cloning and functional analysis of 9-*cis*-epoxycarotenoid dioxygenase (NCED) genes encoding a key enzyme during abscisic acid biosynthesis from peach and grape fruits. *Journal of Plant Physiology* **166,** 1241–1252.

Zhang M, Yuan B, Leng P. 2009*a*. The role of ABA in triggering ethylene biosynthesis and ripening of tomato fruit. *Journal of Experimental Botany* **60,** 1579–1588.

Zhao SL, Qi JX, Duan CR, Sun L, Sun YF, Wang YP, Ji K, Chen P, Dai SJ, Leng P. 2012. Expression analysis of the *DkNCED1*, *DkNCED2* and *DkCYP707A1* genes that regulate homeostasis of abscisic acid during the maturation of persimmon fruit. *Journal of Horticultural Science and Biotechnology* **87,** 165–171.

Zhenga Y, Schumakerc KS, Guo Y. 2012. Sumoylation of transcription factor MYB30 by the small ubiquitin-like modifier E3 ligase SIZ1 mediates abscisic acid response in Arabidopsis thaliana. *Proceedings of the National Academy of Sciences, USA* **109,** 12822–12827.

Zhu GH, Liu YG, Ye NH, Liu R, Zhang JH. 2011. Involvement of the abscisic acid catabolic gene *CYP707A2* in the glucose-induced delay in seed germination and post-germination growth of *Arabidopsis. Physiologia Plantarum* **143,** 375–384.