REGULATORY MECHANISMS UNDERLYING ACTIVATION OF ORGAN ABSCISSION

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Abstract: Abscission is a tightly regulated developmental process that initiates in response to endogenous and environmental cues. In an agricultural context, regulation of abscission has substantial effects on crop productivity and quality. Crop domestication often selected against abscission of the fruit, allowing easier harvesting. A better understanding of the mechanisms underlying abscission will, therefore, inform efforts to improve crop breeding and harvesting practices. In this article, we summarize our current knowledge of the various regulatory mechanisms involved in abscission. We first review the regulation of abscission zone cells as they acquire competence in response to abscission signals. We then summarize the regulation of abscission initiation, exploring the phytohormone signals, developmental factors, and environmental cues regulating the initiation of abscission.

Keywords: abscission zone, abscission activation, phytohormone, transcription factor, kinase

1 Introduction

Abscission is a highly programmed developmental process, that allows plants to shed ripe fruit and senescent, injured, infected, or otherwise dispensable organs (Addicott, 1982; Osborne, 1989). Abscission results in the shedding of vegetative and reproductive organs in response to

developmental and environmental cues. In an agronomic context, abscission is a key factor that affects yield and quality of crops. Hunter-gatherers domesticated the wild ancestors of current-day crops by selecting cereals with reduced abscission, thus decreasing seed and fruit dispersal and increasing yield (Lewis et al., 2006; Fuller, 2007; Onishi et al., 2007). The improvement of organ abscission traits is still pursued by crop breeders today (Jiang et al., 2019) and has been extended to include horticultural crops such as fruits, vegetables, and flowers. For example, in tomato (*Solanum lycopersicum*), *jointless* mutants are characterized by defective development of the pedicel abscission zone (AZ) (Mao et al., 2000). The pedicels (or stems connecting the fruits to the rest of the plant) normally remain attached to the fruit in jointed tomato varieties. In *jointless* mutants, the pedicel AZ does not form, even though AZs between other organ boundaries such as at the base of the leaf or the calyx (sepals) are unaffected. Commercially, this trait has been introduced into many tomato varieties by classical breeding, since during mechanical harvesting of *jointless* tomato fruits, the pedicel separates from the fruit and remains attached to the parent plant, thus preventing damage to other fruits during picking and packing.

Many fruit-bearing trees produce abundant flowers to maximize population survival by generating large numbers of fruits and seeds. During fruit setting, most flowers and young fruits are shed as the mother plant cannot sustain their growth until they reach maturity: this is the so-called physiological fruit drop. In fruit production, excessive abscission results in uneconomical fruit production. Conversely, too little abscission may lead to overloading of the mother plant, which may bear large numbers of fruits with small sizes (Estornell et al., 2013; Tranbarger and Tadeo, 2020). For instance, litchi (*Litchi chinensis*) plants produce many inflorescences with 100–250 female flowers per inflorescence. However, over 95% of the initial female flowers cannot develop into mature fruits following three distinct waves of abscission (Stern et al., 1995; Mitra et al., 2005). In such cases, reducing the proportion of flowers/fruitlets by abscission is a major goal in fruit crop breeding to increase productivity while not overburdening the mother plant (Yuan and Huang, 1988; Mitra et al., 2005).

In ornamental crops, such as roses (*Rosa* sp.) and lilies (*Lilium longiflorum*), how long a flower remains intact before petals start to fall off due to abscission affects 'vase life' and thus is a critical factor in the determination of their ornamental value (Lombardi et al., 2015; Gao et al., 2019). Therefore, rose cultivars that were prone to early petal abscission have gradually become obsolete over the course of cut rose breeding.

A generally accepted model for the abscission process includes four phases (Bleecker and Patterson, 1997; Patterson, 2001; Estornell et al., 2013): phase A, undifferentiated cells differentiate into an anatomically discrete AZ; phase B, the AZ acquires the competence to respond to abscission signals; phase C, the AZ cells are activated by abscission signals, leading to cell separation;

and phase D, which partially overlaps with phase C, the remaining portion of the AZ on the plant trans-differentiates into a protective layer. After the AZ has formed (phase A), it may stay in a quiescent state from days to months until the AZ becomes competent (phase B) to respond to signals as noted above. Therefore, phases B and C are tightly associated with the timing of abscission initiation.

Over the past several decades, genetic and mutational studies, especially with model plants such as Arabidopsis (*Arabidopsis thaliana*) and tomato (*Solanum lycopersicum*), have identified many of the molecular components involved in the regulation of organ abscission activity. In this article, we summarize recent advances on the regulatory mechanisms underlying phases B and C of abscission. We initially address the regulation of AZ cells acquiring the competence to respond to abscission signals and then delve into the regulation of activation of abscission. Of particular interest are the influence of phytohormones, plant developmental stages, and environmental cues on these two critical phases.

2 Acquisition of Competence for Abscission Activation

The role of ethylene in the abscission process was inadvertently discovered almost a century ago (Abeles et al., 1992), while our knowledge of a role for auxin in abscission dates back over 50 years (Addicott, 1982). A commonly accepted model posits that abscission cannot occur when a continuous polar flow of auxin passes through the AZ. Auxin depletion renders the AZ sensitive to ethylene signals for the initiation of abscission. The depletion of auxin flow through the AZ may be a consequence of decreased biosynthesis in the source tissue (abscising organ), or inhibition of polar auxin transport (Bangerth, 1989; Dhanalakshmi et al., 2003; Blanusa et al., 2005; Dal Cin et al., 2009; Celton et al., 2014; Kuhn et al., 2014; Meir et al., 2015).

As early as in 1936, it was demonstrated that in *Coleus*, application of auxin onto petioles with excised leaf blades delayed petiole abscission (La Rue, 1936). Later, Louie and Addicott (1970) reported that in cotton (*Gossypium hirsutum*), auxin applied onto the distal side of the cut petiole inhibited petiole abscission, as expected. However, auxin applied to the proximal side of the stem accelerated the onset of abscission instead (Louie and Addicott, 1970). These observations suggested that the reversal of the auxin gradient across the AZ is critical for the initiation of abscission. Intriguingly, the application of auxin at both the distal and proximal sides of the stem at various concentrations and ratios between the two sides indicated that the magnitude of the auxin gradient across the AZ determined the rate of abscission, not the absolute amount of auxin flowing through the AZ (Louie and Addicott, 1970).

2.1 Auxin Functions in Floral Organ Abscission

Auxin depletion has been documented during various stages of plant growth and development, leading to the detachment of senescing leaves and flowers, and fruits following their ripening. During floral organ abscission, the shedding of unfertilized or male flowers may be ascribed to the low levels of endogenous auxin produced by the ovary (van Doorn and Stead, 1997). In begonia (*Begonia × semperflorens-cultorum*), abscising male flower buds accumulate much lower auxin levels than nonabscising female flowers, and the seasonal variation in male bud shedding coincides with a reduction of the auxin indole-3-acetic acid (IAA) contents in the buds (Hanischtencate et al., 1975). In the Easter lily (*L. longiflorum*), two closely related genotypes showed obvious differences in the context of petal wilting/abscission. The tepals of *L. longiflorum* wilted substantially during senescence but did not shed, whereas the tepals of *L. longiflorum* Asiatic hybrid (L.A.) abscised turgid (Lombardi et al., 2015). Auxin levels correlated with the observed level of floral organ abscission and wilting, with high auxin content in *L. longiflorum*, but much lower auxin levels in the tepals of *Lilium* L.A. (Lombardi et al., 2015). An auxin gradient across the AZ has also been observed during abscission for the pedicel AZ in tomato and the petal AZ in roses. In tomato, the auxin distribution in the pedicel AZ was determined using the synthetic auxin-responsive promoter *DR5* driving the expression of the β-*glucuronidase* reporter gene in the *DR5pro : GUS* construct (Ma et al., 2015). In rose, an immunofluorescence assay using an anti-IAA monoclonal antibody allowed the visualization of auxin distribution during petal abscission (Liang et al., 2020). Both studies demonstrated that the transport of auxin through the AZ decreases during the process of organ abscission. In a petal abscission-prone rose cultivar (*R. hybrida* cv. Golden Shower), petals shed without wilting. Application of exogenous auxin onto the flowers of this cultivar induced petal wilting, but prevented their abscission (Liang et al., 2020).

In cut flowers from the orchid *Dendrobium*, the floral buds at the top of the inflorescence stalk exhibit early yellowing and abscised. Application of an auxin transport inhibitor or an auxin action inhibitor to the stigma of open flowers induced high flower abscission rates (Rungruchkanont et al., 2007). In yellow lupine (*Lupinus luteus* L.), disturbing polar auxin transport caused a reversal of the spatial gradient of IAA, and led to flower abscission (Kucko et al., 2020). In tomato, removal of the flower from the pedicel triggered the abscission of the remaining pedicel. Exogenous auxin placed on the cut surface of the pedicel counteracted the effect of flower removal (Meir et al., 2010). Several additional reports have shown that exogenously applied auxin prevented or delayed abscission of flowers and floral parts such as styles and stamens (van Doorn and Stead, 1997). Accordingly, exogenous auxin treatments can extend the vase life of many cut flowers, such as in *Dendrobium*, Geraldton wax flower (*Chamelaucium uncinatum*), and poinsettia (*Euphorbia*

pulcherrima) (Gilbert and Sink, 1971; van Doorn and Stead, 1997; Abebie et al., 2008).

The modulation of auxin flow results from changes in the transcript abundance of many genes involved in auxin biosynthesis, signal transduction, and transport. The functions of auxin pathway genes on floral organ abscission have been widely investigated. Endogenous auxin levels may be modulated by expressing the bacterial genes *iaaL* and *iaaM*: the encoded iaaL enzyme converts endogenous IAA into its inactive conjugated form IAA-Lys, whereas iaaM catalyses the conversion of Trp into an IAA precursor. In Arabidopsis, manipulation of auxin levels specifically within the floral organ AZ can be accomplished by expressing *iaaL* and *iaaM* under the control of the floral AZ-specific *ARABIDOPSIS DEHISCENCE ZONE POLYGALACTURONASE 2* (*ADPG2*) promoter. The *iaaL* transgenic plants were characterized by lower IAA levels in the floral AZ, resulting in premature shedding. By contrast, *iaaM* transgenic plants showed increased IAA levels and delayed floral organ shedding (Basu et al., 2013).

Turning away from auxin biosynthesis and focusing on auxin signalling components, the proteins encoded by the *Aux/IAA INDUCIBLE* gene family contain a potent transcriptional repression domain and localize to the nucleus via a shared nuclear localization signal. Aux/IAA proteins form heterodimers with Auxin Response Factors (ARFs) transcriptional regulators, which bind to the conserved *cis*-acting Auxin Responsive Element (AuxRE) within auxin-inducible promoters (Roosjen et al., 2018). It was first reported in Arabidopsis that ARF1, ARF2, ARF7, and ARF19 were partially redundant, and functioned in floral organ abscission (Ellis et al., 2005; Okushima et al., 2005). A mutation in *ARF2* alone delayed the onset of floral organ abscission, which was further enhanced by the loss of ARF1 activity, or by the loss of both ARF7 and ARF19 activities (Ellis et al., 2005). In addition, transactivation of the gain-of-function *AXR3-1* gene to disrupt auxin signalling in Arabidopsis floral organ AZ demonstrated a requirement for the IAA signalling pathway to initiate abscission (Basu et al., 2013). Moreover, the expression of the *ARF* gene family was investigated during floral organ abscission in tomato (Guan et al., 2014). The expression of the Aux/IAA gene family during floral organ abscission was investigated in *Mirabilis jalapa* (Meir et al., 2006), *Cestrum elegans* (Abebie et al., 2008), and rose (Gao et al., 2016). The function of Aux/IAA genes involved in floral organ abscission was also tested in rose: the downregulation of *RhIAA16* by virus-induced gene silencing (VIGS) in rose promoted premature petal abscission (Gao et al., 2016).

2.2 Auxin Functions in Ripening-induced Fruit Abscission

Tomato as a model plant for fruit ripening has been widely used to study hormone distribution in fruit during ripening. Auxin levels are high during

the early ripening phase mainly attributed to auxin production in the seeds. Later, auxin levels decrease during ripening and coincides the with maturation of the seeds. Meanwhile, ripening-associated and early auxin-responsive *Gretchen Hagen 3* (*GH3*) genes may function in decreasing the free IAA concentration, and the low auxin levels in the remaining fruit tissues may be an effect of their action (Kumar et al., 2014). The corresponding changes in fruit auxin content are then thought to influence the auxin gradient in the pedicel AZ, since polar auxin transport originates from the fruit. It is intriguing that floral organs are shed following pollination, even though ovules still express *AUXIN SYNTHASE* genes at relatively high levels, which should sustain high auxin levels and thus prevent organ abscission. One possible explanation suggests the existence of a block in the auxin transport in useless floral organs including petals, and stamens, which become obsolete after successful pollination.

To date, four auxin transporter families have been reported, including AUX/LAX (AUXIN1/LIKE-AUX1), PIN (PIN-FORMED, auxin efflux carriers), ABCB (ATP-binding cassette-B (ABCB)/P-glycoprotein (PGP)), and PILS (PIN-Likes) (Zazimalova et al., 2010; Barbez et al., 2012). In tomato, ribonucleic acid (RNA) interference-mediated silencing of *PIN1* expression accelerated pedicel abscission by simultaneously raising auxin accumulation in the ovary and decreasing the auxin content in the AZ (Shi et al., 2017), suggesting that auxin transport mediates the source-sink auxin balance to influence organ abscission.

2.3 Auxin Functions in Leaf Abscission

Leaf abscission takes a relatively long time compared with floral organ abscission, and no functional AZ forms at the base of the leaf in monocots and annual dicots, such as the model plants rice (*Oryza sativa*) and Arabidopsis respectively. The leaves senesce and wilt on the plant, but do not abscise. This phenomenon is termed as marcescence (Meir et al., 2015), and restricts research dedicated to the elucidation of leaf abscission.

In *Populus* (*Populus trichocarpa*), the auxin-responsive reporter *GH3 : GUS* revealed changes in auxin content during the dark-induced abscission of leaves (Jin et al., 2015). The *GH3 : GUS* reporter showed a strong signal before the beginning of the shading treatment, but became much weaker after transfer into shade. Intriguingly, with the shading treatment, a new local auxin response maximum emerged on the abaxial side of the petiole upon shading, and gradually expanded to the adaxial side of the petiole preceding the formation and maturation of the AZ. In addition, application of auxin delayed dark-induced leaf abscission of *Populus* (Jin et al., 2015). Similarly, application of auxin can delay petiole abscission in *Coleus* and cotton (La Rue, 1936; Louie and Addicott, 1970). In tomato, a gene encoding a KNOTTED1-LIKE HOMEOBOX PROTEIN1 (KD1) regulates

ethylene-induced petiole abscission through modulating expression of genes related to auxin transport and signalling components in the petiole AZ (Ma et al., 2015). In addition, a recent study showed that hydrogen sulfide (H_2S) can inhibit ethylene-induced petiole abscission through modulating the expression of genes related to auxin signalling components (Liu et al., 2020). However, the mechanisms of KD1 and H_2S regulating the genes involved in auxin transport and signalling need to be clarified.

2.4 Regulation of the Establishment of Competence

How is abscission competence established? Two possible mechanisms differ in the extent of cellular differentiation and the number of cells receptive to abscission signal(s): (i) the entire separation layer may be pre-differentiated to sense changes in the auxin gradient, or (ii) alternatively only a few cells within the separation layer sense the changing of auxin gradient and then these cells radially secrete a secondary signal outwards. In impatiens (*Impatiens sultani*), small fragments originating from the dissection of a petiole AZ cross-section retained the ability to undergo cell separation independently of the other fragments (Sexton, 1979). In tomato, cortical cells from the leaf AZ abscised after exposure to ethylene even after being dissected away from vascular cells (Tucker and Yang, 2012). These results suggest that cell-to-cell interaction within the AZ is not a prerequisite for organ shedding, and that the cells within the separation layer across the entire petiole are pre-differentiated to abscise.

Bean (*Phaseolus vulgaris*) produces a diffusible signal within the vascular tissue of the leaf AZ to induce separation via leaf cortex cells (Thompson and Osborne, 1994). These results indicated that a few cells within the separation layer establish abscission competence by perceiving the decline in the auxin gradient and transducing the signal to other cells of the separation layer to initiate abscission. An analysis of the auxin gradient in tomato pedicel AZ using the *DR5 : GUS* auxin-responsive reporter system showed that auxin signals were detected in vascular tissue of the AZ (Ma et al., 2015; Shi et al., 2017). Therefore, it is reasonable to speculate that cells in the vascular tissue may constitute the first sensory target of the auxin gradient, assuming that the auxin gradient is the critical factor that establishes abscission competence.

3 Phytohormones Regulate the Activation of Organ Abscission

In addition to the role of auxin in establishing competence in the AZ, phytohormones have major roles in regulating the activation of organ abscission. Some phytohormones such as gibberellin (GA), and brassinosteroid

(BR), inhibit abscission; other phytohormones such as ethylene, abscisic acid (ABA), jasmonic acid (JA), and cytokinin (CTK), accelerate abscission (Estornell et al., 2013; Patharkar and Walker, 2019).

3.1 Other Abscission-inhibiting Phytohormones

GA has been described as an inhibitor of fruit abscission. In peach (*Prunus persica*), exogenous applications of GA blocked fruit shedding (Stutte and Gage, 1990). In *citrus*, pollination increased GA levels in the ovary, leading to inhibition of fruit abscission (BenCheikh et al., 1997; Mahouachi et al., 2009). Fruitlet abscission induced by defoliation reduced carbohydrate contents by removing the major source of photosynthates but did not affect GA levels (Mehouachi et al., 2000). Few studies have explored the role of BRs in organ abscission. In *citrus*, exogenous BR treatment inhibited leaf and fruit abscission, suggesting an inhibitory role for BRs in organ abscission (Iwahori et al., 1990).

3.2 Abscission-accelerating Phytohormones

Ethylene plays a main role as positive regulator of abscission and senescence. Genes involved in ethylene biosynthesis and signal transduction participate in the regulation of organ abscission. In Arabidopsis, the mutants *ethylene-insensitive 2* (*ein2*) and *ethylene response 1* (*etr1-1*) inhibit floral organ abscission (Patterson and Bleecker, 2004). Similarly, the tomato ethylene receptor mutants, *never ripe* (*nr*), *sletr1-1*, and *sletr1-2*, affect ethylene receptor function and ethylene sensitivity, thereby delay fruit ripening and organ abscission (Lanahan et al., 1994; Whitelaw et al., 2002; Okabe et al., 2011). In the wishbone flower (*Torenia fournieri*), heterologous expression of a mutated carnation (*Dianthus caryophyllus*) ethylene receptor gene *Dc-ETR1nr*, that confers ethylene insensitivity, inhibited petal abscission (Tanase et al., 2011). Other examples of ethylene receptors functioning in organ abscission have been reported in peach (*P. persica*), larkspur (*Delphinium* spp.), and mango (*Mangifera indica*) (Rasori et al., 2002; Kuroda et al., 2003; Ish-Shalom et al., 2011). In addition, in tomato, reducing the expression of the *EIN3*-like gene *LeEIL* retarded flower pedicel abscission and fruit ripening (Tieman et al., 2001). *EIN3* encodes a transcription factor that acts downstream of the ethylene pathway to modulate gene expression. In litchi, the expression of *EIN3*-like genes *LcEIL2/3* is strongly upregulated during ethylene-induced fruitlet abscission. Heterologous expression of *LcEIL2/3* in wild-type Arabidopsis and the double *ein3 eil1* mutants accelerated floral organ abscission. LcEIL2/3 directly induced the expression of genes involved in cell wall remodelling, such as the cellulases *LcCEL2/8* and the polygalacturonases *LcPG1/2*, as well as the ethylene biosynthetic genes ACC synthase *LcACS1/4/7* and ACC oxidase *LcACO2/3* (Ma et al., 2020).

ABA was originally isolated from young cotton fruits, and called abscisin II, since it accumulated during abscission (Ohkuma et al., 1963). High levels of ABA in floral organs and fruit AZs prior to abscission have been reported in many plant species (Sagee and Erner, 1991; Vernieri et al., 1992; Zacarias et al., 1995). Therefore, ABA was previously assumed to be directly associated with abscission. However, ABA is now mostly considered to be associated with the activation of organ senescence rather than abscission itself. In *citrus*, exogenous ABA treatment did not affect abscission in intact plants. However, high amounts of ABA did promote ethylene biosynthesis and accelerated abscission in aged or injured detached tissues (Goren, 1993). Similarly, exogenous ABA treatment had no effect on abscission in blue flax (*Linum lewisii*) (Addicott, 1977) and montbretia (*Crocosmia × crocosmiiflora*) (Mckenzie and Lovell, 1992).

The effects of ABA on abscission appear to be dependent on interactions with other phytohormones rather than ABA itself (Estornell et al., 2013). In *citrus*, ABA may induce accumulation of the ethylene precursor 1-aminocyclopropane-1-carboxylic acid (ACC), leading to ethylene biosynthesis and fruit abscission (Gomez-Cadenas et al., 2000). In apple (*Malus domestica*), ABA accumulated in the cortex of abscising fruitlets but not in nonabscising fruitlets. ABA may cooperate with other phytohormones, resulting in the downstream activation of the AZ (Eccher et al., 2013). In Arabidopsis, ABA and JA are both required to induce the expression of the *QUARTET2* gene, which encodes a polygalacturonase, during floral organ abscission (Ogawa et al., 2009).

JA has been reported to accelerate abscission. Exogenous methyl jasmonate treatments induced leaf abscission in bean (Ueda, 1996), as well as fruit abscission in *citrus*, apple, and tomato (Hartmond et al., 2000; Beno-Moualem et al., 2004; Dal Cin et al., 2007). In Arabidopsis, MADS-box transcription factor *AGAMOUS* (*AG*) mutant *ag-1*, exhibited delayed sepal senescence and abscission, and reduced JA content in the flower of *ag-1*. Other mutants deficient in JA, *defective in anther dehiscence 1* (*dad1*) and *delayed dehiscence 2* (*dde2*), exhibited delayed sepal senescence and abscission as well. Exogenous methyl jasmonate treatments rescued the abscission phenotypes of *ag-1*, *dad1* and *dde2* flowers, demonstrating the role of JA in organ abscission (Jibran et al., 2017).

CTKs may promote abscission, although high CTK concentrations can also inhibit abscission (Pierik and Abbadi, 1972; Trueman, 2010). A synthetic CTK-like chemical thidiazuron (TDZ) has been widely used as defoliant to facilitate mechanical harvesting for many crops, especially cotton (Xu et al., 2019). Although the exact mode of TDZ action is not understood, it has been demonstrated that a higher concentration of TDZ application increased ethylene accumulation in cotton, which resulted in leaf abscission (Suttle, 1986). Several other studies also suggest that CTK crosstalks with ethylene to regulate organ abscission (Dal Cin et al., 2007; Xu et al., 2019). It appears that

CTKs may play indirect roles on abscission, depending on interactions with other hormones.

3.3 Crosstalk of Phytohormones in Abscission

3.3.1 Auxin and Ethylene Crosstalk

Unlike the synergistic interaction between auxin and ethylene in controlling specific growth and developmental processes, such as root elongation and root hair formation (Muday et al., 2012), the antagonistic effects of auxin and ethylene on organ abscission have been well established by classical physiological experiments (Addicott, 1982; Sexton et al., 1985). The auxin-ethylene interaction is outlined in a model originally proposed by Rubinstein and Leopold (1963) with regard to organ abscission, and subsequently further demonstrated by Abeles and Rubinstein (1964) and Sexton and Roberts (1982) (Rubinstein and Leopold, 1963; Abeles and Rubinstein, 1964; Sexton and Roberts, 1982). However, to date, the molecular mechanisms underlying the acquisition of ethylene sensitivity in response to auxin deficiency in the AZ are still far from understood. Changes in the transcriptome of the pedicel AZ were investigated in tomato during the rapid acquisition of ethylene sensitivity following flower removal. The results suggested that acquisition of ethylene sensitivity in the AZ was associated with expression changes of auxin-related genes caused by auxin depletion (Meir et al., 2010). Ethylene has been shown to affect auxin levels by either inhibiting auxin transport to the AZ (Morgan and Gausman, 1966; Riov and Goren, 1979) or by increasing the rate of the auxin conjugation to reduce active IAAs (Beyer and Morgan, 1970; Ernest and Valdovinos, 1971; Riov and Goren, 1979). Interestingly, in tomato, application of 1-Methylcyclopropene (1-MCP), an ethylene inhibitor, downregulated expression of the auxin transporter *SlPIN1* and delayed flower abscission, suggesting that ethylene may positively regulate transcription of *SlPIN1* and auxin efflux to affect the flower abscission process (Shi et al., 2017).

3.3.2 Ethylene and ABA Crosstalk

ABA and ethylene are both accelerators of abscission. ABA and ethylene signals are integrated to mediate plant growth and development, as well as plant responses to biotic and abiotic stresses (Zhu and Guo, 2008; Ton et al., 2009; Zhang et al., 2009; Zhao and Guo, 2011; Luo et al., 2014). Similarly, it was shown that in *citrus*, ABA acts as a modulator of ACC levels, leading to the accumulation of ethylene during abscission (Gomez-Cadenas et al., 2000).

3.3.3 Ethylene and JA Crosstalk

Several studies have described the antagonistic or synergistic roles of JA and ethylene in plant development and defence (Lorenzo et al., 2003;

Memelink, 2009; Zhu et al., 2011b). In the context of organ abscission, reduction of JA levels observed in the *ein2* ethylene-insensitive mutants caused an ethylene response with accelerated abscission (Kim et al., 2013). In addition, a double mutant between the JA receptor mutant *delayed abscission 4* (*dab4-1*, also called *coronatine insensitive 1* (*coi1*)) and *ein2-1* rescued ethylene sensitivity for floral organ abscission (Kim et al., 2013; Kim, 2014). These results indicated that JA acts as a negative regulator of ethylene signalling in the context of organ abscission.

4 Developmental and Environmental Cues Alter the Activation of Organ Abscission

Organ abscission is a highly programmed process that simultaneously responds to endogenous (physiological modifications) and exogenous (seasonal changes in the environment) cues (Taylor and Whitelaw, 2001; Sawicki et al., 2015). Here, we summarize the effects of prominent endogenous and exogenous cues on organ abscission.

4.1 Senescence

Abscission is frequently coupled with senescence as both processes are activated by many of the same developmental and environmental factors. Abscission is typically the terminal phase of senescence, while abscission can also take place in the absence of senescence, and vice versa. Ethylene is the major phytohormone that regulates both abscission and senescence. Therefore, mutants in ethylene-related genes may affect both processes and exhibit phenotypes related to abscission and/or senescence, as in the Arabidopsis ethylene-insensitive mutants *etr1-1* and *ein2-1* (Patterson and Bleecker, 2004). In addition, the ectopic expression of the MADS-box transcription factors *AGAMOUS-like 15* (*AGL15*), *AGL18*, and *Forever Young Flower* (*FYF*) in Arabidopsis influenced flower senescence as well as floral organ abscission (Fernandez et al., 2000; Fang and Fernandez, 2002; Adamczyk et al., 2007; Chen et al., 2011b; Chen et al., 2015). However, many genes related to abscission do not necessarily affect the process of senescence, which is especially true for genes with high expression in the AZ. For example, in Arabidopsis, *Inflorescence Deficient in Abscission* (*IDA*) and *NEVERSHED* (*NEV*) regulate floral organ abscission without affecting flower senescence (Butenko et al., 2003; Liljegren et al., 2009).

4.2 Pollination

In many plants, the abscission of floral organs and fruits is tightly linked to reproductive development events such as pollination and fruit ripening.

For example, floral organs begin to shed after pollination. The systematic signals generated by the act of pollination should simultaneously guarantee fruit bearing, while also initiate the detachment of obsolete floral organs like petals and stamens (Kim, 2014). In addition, nutrient mobilization between pollinated flowers (sink tissues) and the rest of the plant (source) takes place up until abscission (Jones, 2013). Ethylene has been suggested as one such systematic signal since an ethylene burst after pollination accelerates abscission (van Doorn and Woltering, 2008; Jones, 2013). We still do not know how the accumulation of post-pollination ethylene accelerates floral organ shedding and not that of fruits. Other developmental factors may underlie and coordinate distinct fruit and floral organ shedding, besides nutrition mobilization and ethylene production.

4.3 Carbohydrates

Abscission often proceeds following the deprivation of, or the competition for, limited carbohydrates/photo-assimilates (Addicott and Lynch, 1955). A major decline in carbohydrate levels in abscising organs has been observed in several plant species, including rose (Borochov et al., 1976), pepper (*Capsicum annuum*) (Aloni et al., 1997), *citrus* (Gomez-Cadenas et al., 2000), apple (Zhu et al., 2011a), and litchi (Peng et al., 2013). In *Dendrobium* and pepper, sucrose feeding can inhibit flower abscission (Aloni et al., 1997; Pattaravayo et al., 2013). Both photosynthesis and the management of carbohydrate reserves can affect organ abscission. In pepper, abscission-prone and abscission-resistant cultivars differ in their potential for sucrose production and starch accumulation in the light (Aloni et al., 1996; Marcelis et al., 2004). In citrus, defoliation treatments at anthesis induced fruit abscission due to a shortage of carbohydrates (Gomez-Cadenas et al., 2000; Iglesias et al., 2003). In apple, the frequency of fruit abscission is inversely correlated with the number of leaves borne by the shoot carrying the fruits (Atkinson et al., 2002; Iwanami et al., 2012). Interestingly, it was reported that sugar levels regulate transcript levels of an auxin biosynthesis gene *ZmYUC* in developing seeds and modulate kernel growth by altering auxin biosynthesis (LeClere et al., 2010).

Organ AZs are located between source and sink organs. Carbohydrates transported from source to sink organs thus pass through the phloem of the AZ. It is, therefore, reasonable to assume that carbohydrate transport may play a key role in the determination of organ sensitivity toward abscission. Indeed, a decrease of the glucose gradient in the pedicel AZ in apple triggered fruit abscission (Beruter and Droz, 1991). We also observed that the transport of sucrose to petals through the phloem of the AZ decreased during petal shedding in rose. In addition, sucrose transport during petal abscission is regulated by auxin via the RhARF7-RhSUC2 module (Liang et al., 2020).

4.4 Reactive Oxygen Species (ROS)

Reactive Oxygen Species (ROS) accumulates in response to abiotic and biotic stresses such as low temperature, drought, salt, and pathogen attack (Baxter et al., 2014). ROS are known to induce organ abscission, and ROS scavengers inhibit organ abscission (Michaeli et al., 1999; Michaeli et al., 2001; Sakamoto et al., 2008b). In apple, fruitlet abscission along the cortex cell layer may be orchestrated by an interaction between phytohormones (ABA and ethylene) and other signal molecules like ROS (Botton et al., 2011; Eccher et al., 2013). It was reported that ethylene can induce ROS production during the abscission process. In tobacco (*Nicotiana tabacum*), peroxidase activity increased during ethylene-induced pedicel abscission (Henry et al., 1974). In the *Capsicum* genus, it was also reported that hydrogen peroxide (H_2O_2) contributes to ethylene-induced leaf abscission (Sakamoto et al., 2008a). Interestingly, in olive (*Olea europaea*), ROS induced abscission in response to ethylene but only in leaves and not in fruits (Goldental-Cohen et al., 2017).

4.5 Light

Light quality and quantity are critical for light-mediated plant development, known as photomorphogenesis. Incubation in the dark, as well as low-light treatments, both induce flower and fruit abscission in several plants, including apple, cotton, grapevine (*Vitis vinifera*) and pepper (Aloni et al., 1996; Ferree et al., 2001; Marcelis et al., 2004; Zhu et al., 2011b). It has been suggested that phytohormones may be recruited to regulate abscission in response to light stress. It is well-known that auxin plays a critical role in the photomorphogenesis by controlling cell elongation in response to the light environment (Franklin, 2016). For instance, Coleus leaves exhibited increased free auxin production in response to decreasing far-red and increasing red light (Mao et al., 1989).

4.6 Water Stress

Many plant species experience early flower and fruit abscission when subjected to abiotic stresses. Drought diminishes the plant water content and induces premature flower and fruit shedding. A recent study in tomato demonstrated that drought-induced pedicel abscission was regulated by phytosulfokine (PSK), a peptide hormone (Reichardt et al., 2020). Under drought condition, phytaspase 2, a subtilisin-like protease of the phytaspase subtype, generates PSK in tomato pedicels by aspartate-specific processing of the PSK precursor. PSK induces the expression of the cell wall hydrolase *TAPG4* gene to activate pedicel abscission. In addition, the expression of *TAPG4* regulated by PSK is in an auxin- and ethylene-independent manner (Reichardt et al., 2020). However, any interaction between PSK

and auxin- and ethylene-mediated regulation of abscission remains to be investigated.

4.7 Temperature

Hostile temperature-influencing organ abscission is a complex process, depending not only on temperature regime but also different growth stages and different tolerance of genotypes (Sawicki et al., 2015). High temperature leading to accelerate floral organ and fruit abscission has been reported in various plant species, such as cotton, soybean (*Glycine max*), bean, peach, grapevine, apricot (*Prunus armeniaca*), avocado (*Persea americana*), and *citrus* (Sedgley and Annells, 1981; Monterroso and Wien, 1990; Reddy et al., 1992; Rodrigo and Herrero, 2002; Yuan and Burns, 2004; Zhao et al., 2005; Gunes, 2006; Couto et al., 2007; Greer and Weston, 2010; Hoque et al., 2015). In pepper, the changing of ethylene biosynthesis and auxin content and transport in high temperature-induced abscission indicated that the reduction of auxin transport capacity associates with high temperature-induced reproductive organ abscission (Huberman et al., 1997). In addition, in cotton, measurement of nonstructural carbohydrate indicated that decreasing of nonstructural carbohydrate is a key factor for fruit abscission under high temperature and enhanced UV-B radiation conditions (Zhao et al., 2005).

Relative low temperature can either accelerate or delay organ abscission. The most obvious example of low temperature-induced organ abscission is the seasonal shedding of leaves in autumn of temperate regions, which is triggered by changes in photoperiod, temperature, and water availability (Addicott, 1982). In postharvest handling of cut flower, low temperature is normally beneficial for inhibiting abscission. But the natural habitats of plant species determine the effect of temperature on the organ abscission. Temperature below the limitation of the individual species temperature 'window' can cause chilling injury (Reid 1991; Ascough et al., 2005). Recently, a multiple year study found that in tropical regions temperature is particularly important during inflorescence and fruit bunch development, and has an effect later on the ripe fruit abscission timing in oil palm (*Elaeis guineensis*) (Tisné et al., 2020).

5 Regulatory Genes Involved in Activation of Organ Abscission

Over the past three decades, many regulatory genes involved in the activation of abscission have been identified, especially in the context of floral
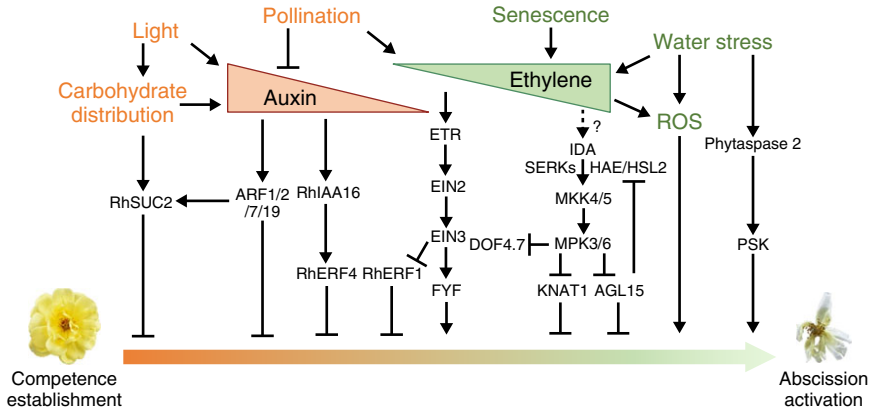
Figure 1 A gene regulatory network that activates floral organ abscission by auxin and ethylene, with the integrated data from multiple species such as Arabidopsis, tomato, and rose.

organ abscission (Figure 1). Here, we summarize most of the regulatory genes involved in the activation of organ abscission, although the relative position of many of these genes along the regulatory pathway is unknown.

5.1 IDA signalling

The last 20 years has witnessed the identification of a regulatory pathway that is essential for floral abscission in Arabidopsis. The receptor-like kinase *RLK5* is expressed specifically in the floral organ AZs. Silencing of *RLK5* (also named *HAESA* (*HAE*)) delayed floral organ abscission (Jinn et al., 2000). In the Arabidopsis *IDA* mutant, most floral organs (petals, sepals, and stamens) remain attached while the silique grows and matures. The *IDA* gene encodes a small protein with an N-terminal signal peptide. *IDA* is part of a small five gene family that are functionally equivalent: indeed, they all accelerated floral organ abscission when constitutively over-expressed (Butenko et al., 2003). IDA peptides bind to the HAE or HAE-LIKE 2 (HSL2) receptors. HAE/HSL2 works with SOMATIC EMBRYOGENESIS RECEPTOR-LIKE KINASE 1/2/3/4 (SERK1/2/3/4) to activate a Mitogen-Activated Protein (MAP) kinase cascade that regulates floral organ abscission (Cho et al., 2008; Stenvik et al., 2008; Meng et al., 2016; Santiago et al., 2016).

A screen for Arabidopsis mutants that restored abscission in the *ida* mutant background identified a KNOTTED-like homeobox gene, *KNAT1*, as a suppressor of the abscission defects seen in *ida*. IDA signalling represses *KNAT1* expression, whose gene product KNAT1 normally induces *KNAT2* and *KNAT6* expression to activate abscission (Shi et al., 2011). Later, the

MADS-domain transcription factor AGL15 was described as a putative regulator of *HAE* expression. Overexpression of *AGL15* resulted in decreased expression of *HAE* as well as a delayed abscission phenotype. MAP kinase-mediated phosphorylation of AGL15 is necessary for full *HAE* expression, suggesting a positive feedback loop controlling *HAE* expression (Patharkar and Walker, 2015). The functions of IDA-like peptides have also been investigated in *citrus*, litchi, lupine, oil palm, and Poplar (Estornell et al., 2015; Stø et al., 2015; Ying et al., 2016; Wilmowicz et al., 2018; Tranbarger et al., 2019).

Several genes and mutants that directly or indirectly affect IDA signal transduction in Arabidopsis have been identified. An ADP-ribosylation factor GTPase-activating protein *NEV* targets the Golgi apparatus and protein secretion, which modulates floral organ abscission (Liljegren et al., 2009). *EVERSHED*, also known as *SUPPESSOR OF BIR1 1* (*SOBIR1*), and *CAST AWAY* (*CST*) encode receptor-like kinases that regulate floral organ abscission, possibly through interference of the IDA signalling pathway (Leslie et al., 2010; Burr et al., 2011; Taylor et al., 2019).

The role of auxin and ethylene in IDA pathway is not addressed, though the regulatory function of IDA in organ abscission has been well established. A recent review re-evaluated the role of IDA in organ abscission based on relevant abscission literatures, and proposed that IDA pathway may be essential for the final stages of organ abscission, while ethylene may play a major role in its initiation and progression (Meir et al., 2019).

5.2 Transcription Factors and Kinases

Nine transcription factor families have been reported to be involved in regulating activation of organ abscission (Table 1). Among them, transcription factors involved in ethylene and auxin signalling pathways have been identified as regulators of abscission activation, including EIN3, ARFs, and Aux/IAAs. MADS-box genes regulate the activation of floral organ and fruit abscission in Arabidopsis, tomato, peach, *Oncidium,* and *Cattleya intermedia* orchids, besides the classic functions of MADS-box transcription factors during formation of the AZ (Mao et al., 2000; Nakano et al., 2012; Liu et al., 2014). In addition, members of KNOTTED-LIKE HOMEOBOX, HD-ZIP, DOF, and Zinc Finger transcription factor families have been found to play important roles in activation of organ abscission. Moreover, genetic and mutational studies in Arabidopsis identified several receptor-like kinases involved in activation of organ abscission, including HAE/HSL2, EVERSHED/SOBIR1, SERKs, and CST (Cho et al., 2008; Leslie et al., 2010; Burr et al., 2011; Meng et al., 2016). A NAK-type protein kinase gene in apple also functions in the activation of organ abscission (Kim et al., 2011).

Table 1 Regulatory genes involved in the activation of organ abscission.

Gene name	Plant species	Function	Reference
MADS-box transcription factor			
AGL15	Arabidopsis	Floral organ abscission	Fernandez et al. (2000), Fang and Fernandez (2002)
AGL18	Arabidopsis	Floral organ abscission	Adamczyk et al. (2007)
FYF	Arabidopsis	Floral organ abscission	Chen et al., (2011b), Chen et al. (2015)
AGAMOUS	Arabidopsis	Floral organ abscission	Jibran et al. (2017)
PpMADS4	Peach	Floral organ abscission	Xu et al. (2008)
OoFYF	Oncidium orchid	Floral organ abscission	Chen et al. (2011a)
CaFYF1/2	Cattleya intermedia	Floral organ abscission	Chen et al. (2018)
SlFYFL	Tomato	Fruit abscission	Xie et al. (2014)
EIN 3 transcription factor			
LeEIL	Tomato	Floral organ abscission	Tieman et al. (2001)
LcEIL2/3	Litchi	Fruit abscission	Ma et al. (2020)
AP2/EREBP transcription factor			
SHN	Arabidopsis	Protective layer formation	Aharoni et al. (2004)
EDF1/2/3/4	Arabidopsis	Floral organ abscission	Chen et al. (2015)
SlERF52	Tomato	Floral organ abscission	Nakano et al. (2014)
RhERF1	Rose	Floral organ abscission	Gao et al. (2019)
RhERF4	Rose	Floral organ abscission	Gao et al. (2019)
KNOTTED-LIKE HOMEOBOX transcription factor			
KNAT1	Arabidopsis	Floral organ abscission	Shi et al. (2011)
KNAT2/6	Arabidopsis	Floral organ abscission	Shi et al. (2011)
KD1	Tomato	Floral organ abscission	Ma et al. (2015)
LcKNAT1	Litchi	Fruit abscission	Zhao et al. (2020)
HD-ZIP transcription factor			
LcHB2/3	Litchi	Fruit abscission	Ma et al. (2019)
SlREV	Tomato	Floral organ abscission	Hu et al. (2014)
DOF transcription factor			
AtDOF4.7	Arabidopsis	Floral organ abscission	Wei et al. (2010, Wang et al. (2016)
Zinc finger transcription factor			
AtZFP2	Arabidopsis	Floral organ abscission	Cai and Lashbrook (2008)
ARF transcription factor			
ARF1	Arabidopsis	Floral organ abscission	Ellis et al. (2005)
ARF2	Arabidopsis	Floral organ abscission	Ellis et al. (2005), Okushima et al. (2005)
ARF7	Arabidopsis	Floral organ abscission	Ellis et al. (2005)
ARF19	Arabidopsis	Floral organ abscission	Ellis et al. (2005)
Aux/IAA transcription factor			
RhIAA16	Rose	Floral organ abscission	Gao et al. (2016)

(continued overleaf)

Table 1 (*continued*)

Gene name	Plant species	Function	Reference
Receptor-like kinase			
HAE/HSL2	Arabidopsis	Floral organ abscission	Cho et al. (2008), Stenvik et al. (2008)
EVERSHED/SOBIR1	Arabidopsis	Floral organ abscission	Leslie et al. (2010), Taylor et al. (2019)
SERK1/2/3/4	Arabidopsis	Floral organ abscission	Lewis et al. (2010), Meng et al. (2016)
CST	Arabidopsis	Floral organ abscission	Burr et al. (2011)
NAK-type protein kinase			
AFSK	Apple	Floral organ abscission	Kim et al. (2011)

6 Concluding Remarks and Perspectives

Over the last decades, genetic and mutational studies have identified many molecular components involved in the regulation of organ abscission activation. Although no single common mechanism fits all the types of abscission, auxin appears to be a critical component for most abscission types. It is well established that an auxin gradient across the AZ is critical for the initiation of abscission. However, how AZ cells sense the auxin gradient remains elusive. Further studies should clarify whether changes in the auxin gradient through the AZ is sensed by the entire separation layer or a few cells, which then secrete a secondary signal radially to transmit the abscission signal. Ethylene also plays a major role in accelerating abscission. The interaction between auxin and ethylene signalling during abscission is well established at the physiological level, but a molecular explanation of the classical dogma behind the 'balance between auxin and ethylene in abscission' remains to be offered. The molecular mechanisms leading to ethylene sensitivity in response to auxin deficiency in the AZ are far from understood as well. The roles of phytohormones, and developmental and environmental cues in activation of organ abscission have been extensively investigated. However, further research directions are necessary in order to dissect the interactions between these various cues and the IDA pathway, and how they activate organ abscission.

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