



## FLOWERING NEWSLETTER REVIEW

# Cross-talk between environmental stresses and plant metabolism during reproductive organ abscission

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## Abstract

In plants, flowering is a crucial process for reproductive success and continuity of the species through time. Fruit production requires the perfect development of reproductive structures. Abscission, a natural process, can occur to facilitate shedding of no longer needed, infected, or damaged organs. If stress occurs during flower development, abscission can intervene at flower level, leading to reduced yield. Flower abscission is a highly regulated developmental process simultaneously influenced and activated in response to exogenous (changing environmental conditions, interactions with microorganisms) and endogenous (physiological modifications) stimuli. During climate change, plant communities will be more susceptible to environmental stresses, leading to increased flower and fruit abscission, and consequently a decrease in fruit yield. Understanding the impacts of stress on the reproductive phase is therefore critical for managing future agricultural productivity. Here, current knowledge on flower/fruit abscission is summarized by focusing specifically on effects of environmental stresses leading to this process in woody plants. Many of these stresses impair hormonal balance and/or carbohydrate metabolism, but the exact mechanisms are far from completely known. Hormones are the abscission effectors and the auxin/ethylene balance is of particular importance. The carbohydrate pathway is the result of complex regulatory processes involving the balance between photosynthesis and mobilization of reserves. Hormones and carbohydrates together participate in complex signal transduction systems, especially in response to stress. The available data are discussed in relation to reproductive organ development and the process of abscission.

**Key words:** Carbon metabolism, climate change, environmental stress, flower/fruit abscission, hormonal balance.

## Introduction

Throughout their development, plants are subject to a multiplicity of stresses, which lead to molecular, biochemical, physiological, anatomical, and morphological changes that may adversely affect their growth and productivity (Stopar, 1998). The abscission process has been developed by plants to facilitate the shedding of no longer needed, infected, damaged or senescent organs. This phenomenon can occur in both vegetative and reproductive

organs (González-Carranza *et al.*, 1998; Taylor and Whitelaw, 2001; Estornell *et al.*, 2013).

Abscission is an active physiological process that occurs through the dissolution of cell walls at predetermined positions, the abscission zones (AZs), often related to stress and senescence (Addicott, 1982; Taylor and Whitelaw, 2001). Secretion of hydrolytic enzymes, increased peroxidase activity, and loss of calcium and pectin from the wall

of separation layer cells presumably lead to the dissolution of the pectin-rich middle lamella, weakening the cell wall and leading to disintegration of AZ tissues (Fig. 1; Addicott, 1982; Osborne, 1989; Tripathi *et al.*, 2008). In flower, the AZs are located at the boundary between floral organs and the receptacle (González-Carranza *et al.*, 2002; 2007; Lashbrook and Cai, 2008), but also within the flower pedicel (Zanchin *et al.*, 1995; del Campillo and Bennett, 1996).

Three waves of abscission are recognized in fruit trees and can vary according to species (Fig. 2). Generally, the first wave occurs at blooming or shortly after, following pistil abortion, and consists largely of abnormal and unpollinated flowers. The second wave appears after failure of fertilization (Aloni *et al.*, 1996; Rodrigo and Herrero, 2002; Acar and Kakani, 2010). The third wave, known as ‘June drop’, involves fruitlets and occurs following competition for nutrients (both among fruitlets and between fruitlets and vegetative shoots) and failure of embryo development (Goldschmidt and Koch, 1996; Yuan and Greene, 2000). As discussed later, abscission is a highly regulated developmental process that is simultaneously influenced and activated in response to exogenous (changing environmental conditions, interactions with microorganisms) and endogenous (physiological modifications) stimuli.

During climate change, stressed plant communities will be more susceptible to biotic and abiotic stress (Petoukhov and Semenov, 2010; IPCC, 2013), leading to flower and fruit abscission, and consequently to a decrease in fruit yield. During the activation phase of abscission, phytohormones are well known to be the principal transducers of genetic information that modulates the expression of abscission-related genes (Chandler, 2011; Sauer *et al.*, 2013) (Fig. 1). Carbohydrates may also trigger the response of AZ cells to abscission signals.

This review reports on current information on various factors involved in the abscission of reproductive structures, especially in woody species. A special interest will be devoted to environmental, physiological and molecular changes, at hormone and carbohydrate levels, governing the abscission process in reproductive organs. We will focus on the signal transduction cascades affecting the abscission process in flowers and fruitlets (the abscission of mature fruits, which is better documented, is not discussed).

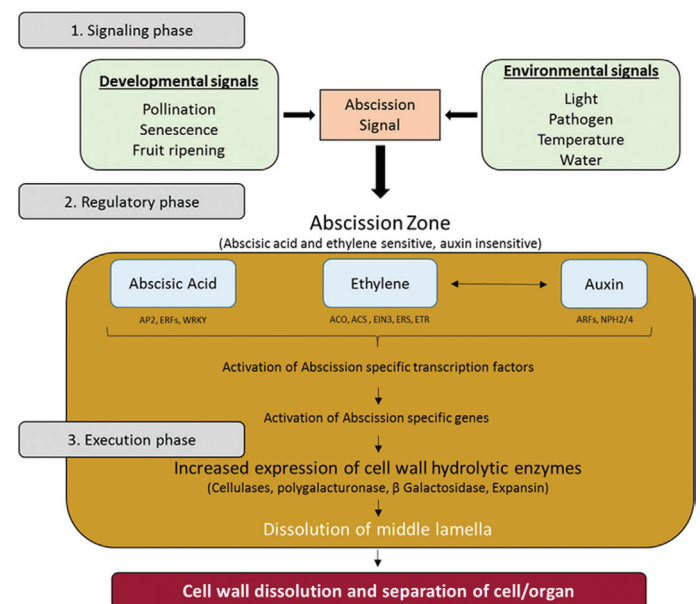
## Impacts of biotic and abiotic stresses on abscission

As sessile organisms, plants are often exposed to unfavourable conditions due to biotic and/or abiotic stresses that can

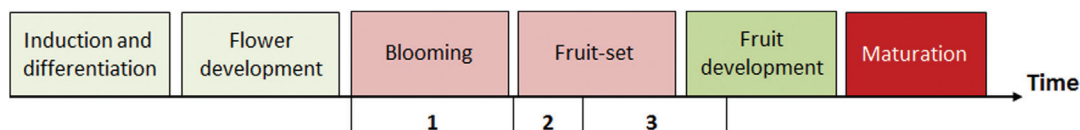
delay growth and development, reduce productivity and, in extreme cases, lead to death.

### Biotic stresses

Following biotic stresses, the activation of the plant immune system, which allows a switch from growth and development into a defensive mode, leads to a lack of nutrients through changes in hormonal and/or carbohydrate content, inducing abscission. Although it is known that biotic stress induce abscission by developmental and physiological modifications (Bergey *et al.*, 1999; Peres *et al.*, 2008; Tripathi *et al.*, 2008), only a few studies have been dedicated to specific effects of biotic stresses on flower abscission. For example, it was suggested that *Citrus* fruit drop induced by *Colletotrichum acutatum* might be due to an alteration of the balance between



**Fig. 1.** A model showing major events leading up to abscission [adapted from Tripathi *et al.* (2008)]. The complete abscission follows three phases. In the signalling phase, formation of the AZ takes place under various developmental and environmental conditions. In the regulatory phase, the AZ is able to perceive different stimuli generated by both external and internal factors and transduced by signals resulting in ethylene/ABA sensitivity and auxin insensitivity in the cell, activating several cascades and transcriptional regulators. In the execution phase, the initiation of abscission starts with the expression of several wall-loosening agents like cellulases, polygalacturonases, or expansin. The collective actions of all these agents accelerate the dissolution of middle lamella. Finally, cell wall dissolution takes place resulting in cell/organ separation. ACO, ACC oxidase; ACS, acyl CoA synthetase; ETR, ethylene response; ERS, ethylene response sensor; EIN3, ETHYLENE INSENSITIVE 3; AP2, ARF, ERF, NPH2/4, and WRKY are transcription factors.



**Fig. 2.** Schematic representation of the three waves of abscission (1, 2, and 3) occurring during the course of flower/fruit development [according to Goldschmidt and Monselise (1977)]. Major processes are indicated.

auxin and related indole compounds (Chung *et al.*, 2003). Due to the limited information available on biotic stresses, these are not discussed further here.

### Abiotic stresses

Abiotic stress factors have a huge impact on world agriculture by reducing average yields for most major crop plants (Wang *et al.*, 2003). At blooming, temperatures (cold/hot), water availability, and light radiation (quality and quantity) are considered as the major causes of abscission.

#### Temperature stress

The ability of plants to cope with hostile temperatures is a complex process, depending not only on the temperature regime, but also on genetic traits, and this has been reported in various species (Bertamini *et al.*, 2007; Ledesma *et al.*, 2008; Acar and Kakani, 2010; Cottee *et al.*, 2010; Greer and Weston, 2010). Many studies reported effects of harmful temperatures (cold/hot) on reproductive organs and subsequent fruit set (Table 1). Briefly, temperature stress can create asynchrony between male and female reproductive development, both of which are required for successful reproduction (Herrero, 2003; Hedhly *et al.*, 2008). For example, warm conditions accelerate anthesis but not pistil development, resulting in flowers with a reduced pistil weight and a shorter style length in apricot (Rodrigo and Herrero, 2002).

#### Water stress

As a result of a decline in plant growth and vigour, water stress might promote organ abscission (Taylor and Whitelaw, 2001). For instance, in Satsuma mandarin, reduced flowering occurs under severe water deficit, and in olive water availability increases flowering and fruit set, and reduces fruit drop (Michelakis, 1989; Lavee *et al.*, 1990). In apple and citrus, water stress during flowering affects the final fruit number per tree, significantly reducing the yield (George and Nissen, 1988; Garcia-Tejero *et al.*, 2010).

#### Light stress

Dark and low-light treatments increase flower and fruit abscission in various species, since light quality and quantity are critical for photomorphogenesis (Taylor and Whitelaw, 2001). In apple, cotton, grapevine, and pepper, shading (30–90%) during reproductive development dramatically increases inflorescence abscission and reduces fruit set (Aloni *et al.*, 1996; Ferree *et al.*, 2001; Marcelis *et al.*, 2004; Zhu *et al.*, 2011).

## Impacts of hormonal balance on abscission

Abiotic stresses trigger many biochemical, molecular, and physiological changes and responses that influence various aspects of cellular and plant metabolism, leading to important

**Table 1.** Effects of temperature stress on reproductive organs in woody species

	Negative effect	Species	Temperature	References
Fruit set	Fruit set decrease	Apricot	>25°C in the pre-blooming period	Rodrigo and Herrero, 2002
		Cherimoya	30/25°C	Higuchi <i>et al.</i> , 1998
		Cotton	40°C	Reddy <i>et al.</i> , 1992
		Peach	32°C	Couto <i>et al.</i> , 2007
		Pear	17°C	Tromp and Borsboom, 1994
		Grapevine	38/33°C from budbreak to after anthesis	Buttrose and Hale, 1973
			19°C<night<35°C	Buttrose, 1974
			>25°C during bloom fruit set period	Kliewer, 1977
			12/9°C one week near flowering	Ebadi <i>et al.</i> , 1995, 1996
			17/12°C	Haeseler and Fleming, 1967;
Sweet cherry	25°C before anthesis	Buttrose and Hale, 1973		
	>20°C	Beppu <i>et al.</i> , 2001		
Development of reproductive structures	Abortive ovule	Apple	<0°C	Hedhly <i>et al.</i> , 2007
		Cherry	<0°C	Simons, 1969
		Plum	20°C at onset of full bloom	Stösser and Anvari, 1982
		Sweet cherry	>20°C	Cerovic <i>et al.</i> , 2000
	Flower abscission	Avocado	25°C before anthesis	Hedhly <i>et al.</i> , 2007
		Grapevine	>28°C	Beppu <i>et al.</i> , 2001
	Flower bud death	Apricot	40/25°C	Sedgley, 1977
			1 h or 3 h at –4°C in the dark at first or full bloom	Greer and Weston, 2010
	Flower drop	Cherimoya	Between –2 and –9°C one night at first or full bloom	Gunes, 2006
			30/25°C	
Fruitlet abscission	Avocado	33/28°C	Higuchi <i>et al.</i> , 1998	
		>30/20°C	Sedgley and Annells, 1981	
		≥32°C daily	Reddy <i>et al.</i> , 1991; Hodges <i>et al.</i> , 1993;	
		36/28°C	Zhao <i>et al.</i> , 2005	

signalling modifications for coping with these unfavourable conditions. Hormones and sugars are particularly important, interconnected molecules, and lead to abscission under stress conditions. The impact of hormonal balance and carbon metabolism on the abscission process will be detailed in the following sections.

In the overall process of abscission, regulatory effects of plant hormones are of major relevance since they mediate responses of plant organs to stress (Peleg and Blumwald, 2011; Estornell *et al.*, 2013; Smékalová *et al.*, 2013). Depending on their concentration in different tissues, the concentrations and affinities of their receptors, their homeostasis, their transport, or their interactions with each other, hormones can act as accelerating or inhibiting signals affecting abscission, and responses are complex. Several hormones, including ethylene, abscisic acid (ABA) and, in specific circumstances, cytokinins, act as abscission-accelerating signals (Sipes and Einset, 1983; Taylor and Whitelaw, 2001; Dal Cin *et al.*, 2007), while auxin, gibberellins (GA), and polyamines are considered as abscission inhibitors (Ben-Cheikh *et al.*, 1997; Taylor and Whitelaw, 2001; Aziz, 2003). Since plant hormones are involved in whole-plant biology, a large number of genes regulating abscission are also part of the hormone biosynthetic and signalling pathways or influence their metabolism.

Though the role of the many hormone families remains ambiguous, ethylene, auxin/ethylene balance and, more recently, ABA have been shown to trigger abscission. Later in this review, it is shown that crosstalk between these molecules is crucial in this process.

### Ethylene

Ethylene biosynthesis increases before abscission in many shedding organs, including reproductive organs (Reid, 1985; Taylor and Whitelaw, 2001; Zhu *et al.*, 2010). In woody plants, a role for ethylene in abscission has largely been

confirmed by application of exogenous ethylene (ethephon) and its precursors (Table 2). Application promotes abscission, while different inhibitors of ethylene biosynthesis reduce it (Williams and Flook, 1980; Bessis *et al.*, 2000; Zhu *et al.*, 2010) (Fig. 3). In apple fruitlets, the induction of abscission with chemical thinner allows a stimulation of ethylene biosynthesis in parallel with the upregulation of key regulatory genes, which lead to the synthesis of 1-aminocyclopropane-1-carboxylic acid (ACC, an ethylene precursor) (Dal Cin *et al.*, 2005, 2007, 2009). This regulation was also reported in grapevine during flower and fruit abscission (Hilt and Bessis, 2003). Moreover, increased expression of *ACO* genes (which encode the enzyme converting ACC to ethylene) as well as *ACO* activity have been reported in organs which undergo abscission (Ruperti *et al.*, 2001; Dal Cin *et al.*, 2005, 2007, 2009). Thus, ethylene biosynthetic and signalling pathways may be involved in abscission.

Ethylene is often characterized as the final effector in the abscission process, triggering the final steps and activating the transcription of genes encoding hydrolytic enzymes and their secretion, responsible for cell wall dissolution in the AZ (Goren, 1993; Bonghi *et al.*, 2000; Zhu *et al.*, 2010). Finally, inhibition of ethylene biosynthesis/action, decreases particularly the ethylene-induced, and more generally stress-induced abscission (Reid, 1985). Nevertheless, the specificity of the AZ in the abscission response also depends on its ability to sense ethylene. Indeed, in some cases, abscission occurs without a rise in ethylene production.

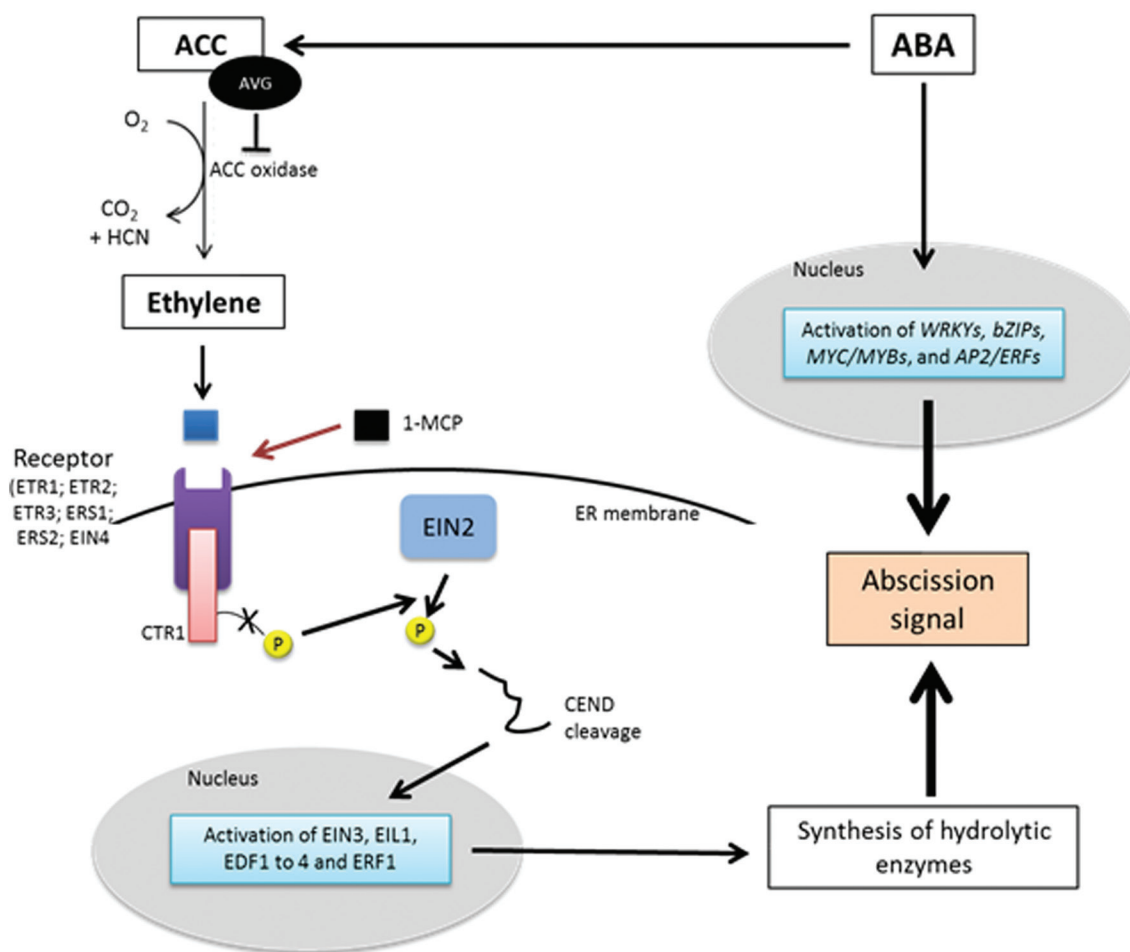
### Auxin

Auxin mediates diverse developmental responses including the control of senescence and organ abscission (Ellis *et al.*, 2005). As for ethylene, the involvement of auxin in abscission was studied using exogenous spraying of auxin or auxin analogues. In 1955, Addicott and Lynch noted that application of indole-3-acetic acid (IAA), able to fulfil most auxin actions

**Table 2.** ABA, auxin and ethylene involvement in flower and fruit abscission

	Effect	Species	References	
Ethylene and precursors	Stylar abscission	Lemon	Sipes and Einset, 1982	
	Flower abscission	Grapevine	Bessis <i>et al.</i> , 2000	
	Fruitlet abscission	Cotton	Lipe and Morgan, 1973	
		Citrus	Goren, 1993	
		Apple	Dal Cin <i>et al.</i> , 2005, 2007, 2009; Yuan and Carbaugh, 2007; Zhu <i>et al.</i> , 2010	
		Grapevine	Bessis <i>et al.</i> , 2000	
		Peach	Rasori <i>et al.</i> , 2002	
		Mango	Malik <i>et al.</i> , 2003	
	Auxins and related	Reduced stylar abscission	Cherry, plum, citrus	Addicott and Lynch, 1955; Einset <i>et al.</i> , 1980
		Reduced fruitlet and fruit drop	Lychee	Stern <i>et al.</i> , 2000; Peng <i>et al.</i> , 2013
		Citrus	Agustí <i>et al.</i> , 2002	
		Apple	Drazeta <i>et al.</i> , 2004; Yuan and Carbaugh 2007	
		Cherry	Else <i>et al.</i> , 2004	
ABA	Flower and fruitlet abscission	Grapevine	Weaver and Pool, 1969	
		Cotton	Gunn, 1982	
		Citrus	Sagee and Erner, 1991; Zacarias <i>et al.</i> , 1995	
		Apple	Vernieri <i>et al.</i> , 1992	





**Fig. 3.** Proposed model leading to activation of the abscission process involving ABA and/or ethylene. Ethylene is recognized by an ethylene receptor, leading to transcriptional activation of genes encoding hydrolytic enzymes. The synthesis of hydrolytic enzymes leads to an abscission signal and finally to cell wall dissolution in the AZ. AVG blocks ethylene synthesis and 1-methylcyclopropene (1-MCP) prevents ethylene recognition by the receptor. In each case, these ethylene inhibitors reduce the abscission signal. ABA acts as the modulator of ACC levels and therefore stimulates ethylene synthesis. Newly synthesized ABA as a result of the perception of environmental stress can also induce the activation of some specific ABA-signalling genes, leading to activation of the abscission signal. AdoMet, S-adenosyl-methionine; CEND: carboxyl end of EIN2; ER, endoplasmic reticulum; CTR1, CONSTITUTIVE TRIPLE RESPONSE 1; EDF1 to 4, ENDOTHELIAL DIFFERENTIATION-RELATED FACTOR 1 to 4; EIL1, ETHYLENE INSENSITIVE-LIKE1; EIN2 to 4, ETHYLENE INSENSITIVE2 to 4; ERS1, ETHYLENE RESPONSE SENSOR 1; ETR1 to 3, ETHYLENE RESPONSE 1 to 3; ERF1, WRKYs, bZIPs, MYC/MYBs, and AP2/ERFs are transcription factors.

(Sauer *et al.*, 2013), retarded abscission of reproductive structures in various species. Investigations in woody species have also reported a decrease of abscission with application of auxin and auxin analogues (Table 2). The currently accepted model for abscission implies that auxin is produced by the subtending organ and is then transported through the AZ, thereby delaying its activation by reducing the sensitivity of the AZ to ethylene (Dhanalakshmi *et al.*, 2003; Blanusa *et al.*, 2005; Meir *et al.*, 2006, 2010). For instance, a decrease in polar auxin transport (PAT) through sweet cherry pedicels, caused by inhibitors of PAT, triggers fruit abscission by increasing the sensitivity of AZ cells to ethylene (Blanusa *et al.*, 2005). In addition, in *Mirabilis jalapa*, some transcripts encoding Aux/IAA proteins, polygalacturonase inhibitor,  $\beta$ -expansin, and  $\beta$ -tubulin, are downregulated by auxin depletion (Meir *et al.*, 2006). Recently, it was reported that 2,4-D sprayed on the canopy of lychee trees leads to a decline in the mRNA level of *LcPGI*, coinciding with a reduced fruitlet abscission

rate (Peng *et al.*, 2013). Moreover, in *Arabidopsis*, Basu *et al.* (2013) showed that auxin regulates the timing of organ abscission and that a functional IAA signalling pathway is required for setting up abscission. These results underline the relationship between auxin depletion/presence and up- and down-regulation of the amount of polygalacturonase mRNA in the AZ, indicating that a critical threshold level of free IAA has to be supplied continuously to the AZ cells for effective and continuous expression of Aux/IAA genes.

Auxin can also be used as a thinning molecule to reduce the competition among fruitlets in many tree species (Table 2). Naphthaleneacetic acid (NAA) application induces ethylene evolution from spurs leading to fruitlet abscission (Currv, 1991; McArtney, 2002), and this is through ethylene biosynthesis and signalling (Zhu *et al.* 2010). Ethylene production might be a consequence of the impaired photosynthetic activity in leaves due to auxin application. Indeed, after treatment with NAA, Weinbaum and Simons (1974) and Schneider

(1975) have reported reduced transport of exogenously applied, labelled sucrose to developing fruitlets in parallel with an increase of ethylene production in fruits. As a consequence, photosynthate availability or transport in fruitlets is reduced, leading to ethylene production and inhibition of PAT through the AZ, and then to abscission (Agustí *et al.*, 2007a; Mesejo *et al.*, 2012). Last, Agustí *et al.* (2007a) have reported that application of 3,5,6-trichloro-2-pyridyloxy-acetic acid (3,5,6-TPA) to whole trees, at the onset of the cell enlargement stage, significantly increased fruitlet abscission; and that this was dependent on the concentration applied, probably due to the higher level of ethylene produced in 3,5,6-TPA-treated fruits. In summary, the auxin status, as well as any factor that affects the supply of auxin to the AZ, control sensitivity of the AZ to ethylene.

### ABA

Although a high level of ABA in the AZ, prior to abscission, has been reported in flowers and fruitlets of many species (Sagee and Erner, 1991; Vernieri *et al.*, 1992; Zacarías *et al.*, 1995), the direct involvement of ABA in the abscission process remains unclear. In *Citrus*, exogenous ABA does not promote abscission in intact plants. However, in aged or injured detached tissues, high amounts of ABA stimulate ethylene synthesis and promote abscission (Goren, 1993). ABA appears to act as the modulator of ACC levels, and therefore of ethylene, leading to increased abscission (Guinn, 1982; Talon *et al.*, 1997; Gómez-Cadenas *et al.*, 2000) (Fig. 3). For instance, nutritional stress in apple fruitlets leads to the activation of some specific ABA-signalling genes during the early phases of abscission (Botton *et al.*, 2011; Eccher *et al.*, 2013) (Fig. 3). Considering these findings, ABA newly synthesized after nutritional stress may be biologically active, acting either directly or indirectly on the abscission process.

### GA

Application of GA significantly delays flower drop and increases fruit set (Mahouachi *et al.*, 2009). Unfortunately no more data are available on the impact of GA on abscission.

### Cytokinins

Cytokinins are mainly known as abscission-accelerating hormones. Indeed, using a stylar abscission bioassay, the timing of explant abscission was hastened when cytokinins were added to the medium (Sipes and Einset, 1983). Studying the possible relationships between cytokinins, ethylene, and abscission, these authors concluded that cytokinins can stimulate *Citrus* abscission *in vitro*. Nevertheless, cytokinins have also been reported as reducers of flower and fruitlet drop, although they are not the most efficient compared to other hormones (Trueman, 2010). Cytokinins were recently used to shed light on the signalling pathways mediating the induction of apple fruitlet abscission. Based on transcriptomic and metabolic data, a hypothetical model has been proposed that suggests a strong link between abscission induction, magnified

by the cytokinin treatment, and the nutritional stress within the tree (Botton *et al.*, 2011; Eccher *et al.*, 2013).

### Brassinosteroids

In Calamondin, Iwahori *et al.*, (1990) have reported that brassinosteroids delay the abscission of fruitlets more strongly than IAA does, probably by increasing the availability of assimilates (Hayat *et al.*, 2000; Gomes *et al.*, 2006).

### Polyamines

The link between polyamines and fruit abscission has been scrutinized particularly closely. Their effects vary according to the polyamine type, concentration, and time of application (Aziz, 2003; Malik and Singh, 2003, 2006; Khezri *et al.*, 2010). For instance, in mango, spermine is probably the most critical polyamine for abscission (Malik and Singh, 2003), while in grapevine inflorescences, an increased percentage of abscission has been correlated with free polyamine levels, mainly spermidine (Aziz *et al.*, 2001; Aziz, 2003). Further, application of specific inhibitors of polyamine pathways induce abscission (Aziz *et al.*, 2001; Malik and Singh, 2003). It has been suggested that spermidine metabolism may influence sucrose synthesis or its accumulation in sink organs, with fruitlet abscission correlating with a low level of polyamine and sugars (Aziz, 2003).

### Crosstalk between hormone families

Reproductive processes are strongly affected by plant growth regulators, indicating that the regulatory mechanism controlling abscission may involve a pivotal hormonal component (Gaspar *et al.*, 2003; Chandler, 2009). For instance, in citrus fruitlets, GA deficiency is associated with a rise in ABA, release of ethylene, and ovary abscission (Zacarías *et al.*, 1995; Iglesias *et al.*, 2007). It has also been shown that GA application accelerates IAA metabolism in citrus, which might explain a reduction in fruitlet drop (Liao *et al.*, 2006). In cotton, it seems that ABA, IAA, and GAs interact to influence both development and abscission of fruitlets (Smith, 1969). So, appropriate changes in auxin levels could either amplify or counteract abscission by accelerating the influence of moderate levels of ABA (Addicott, 1970). In addition, changed ABA content may result from disturbance of PAT (Bangerth, 2000).

### Interaction between environmental stresses and hormonal status

Plant hormones are major signalling molecules under stress leading to adaptation to suboptimal environmental conditions (Santner and Estelle, 2009). However, there is only a little information available on their direct involvement in the abscission of reproductive structures of woody species following environmental stresses. In cotton, water stress increases ethylene and ABA content in young bolls, while it decreases the concentration of free IAA, resulting in boll abscission

(Guinn *et al.*, 1990). In conditions of severe water stress in citrus plants, a rise in ABA promotes the synthesis and accumulation of ACC through the stimulation of ACC synthase activity (Tudela and Primo-Millo, 1992). After plant rehydration, ACC is transported into the xylem stream from roots to aerial organs, where it is metabolized to ethylene; shortly thereafter the abscission process occurs. Thus, water stress-promoted ABA synthesis in roots triggers ethylene production in aerial parts of the plant and causes their abscission.

## Carbohydrates

Under optimal growth conditions, the rate of flower abscission has been correlated with the pathway of both male and female organ development and with the amount of carbohydrates in the flowers (Herrero and Hormaza, 1996; Yu *et al.*, 2000). For instance, abscission can be induced by treatments that reduce or block nutrient supply to the apple fruit AZ (Berüter and Droz, 1991). Further, only fruitlets where the glucose content in the pedicel is below a critical level abscise (Berüter and Droz, 1991), suggesting the presence of a glucose gradient in the AZ similar to auxin. More recently, Peng *et al.* (2013) have shown that carbohydrate shortage leads to dramatically accelerated lychee fruitlet abscission.

In plants, both photosynthetic rate and management of carbohydrate reserves reflect carbon metabolism. Pepper cultivars with distinct susceptibilities to flower abscission might differ in their capacity to produce sucrose and accumulate starch during the light (Aloni *et al.*, 1996; Marcelis *et al.*, 2004). If accumulation of starch during the day is lower, night respiration might deplete a large part of the flower carbohydrate reserves and, thereby, trigger abscission (Preiss, 1982). For instance, in grapevine, 'abscission-sensitive' Gewurztraminer exhibits stronger vegetative growth than 'abscission-tolerant' Pinot Noir, suggesting that flower abscission sensitivity is related to lower sugar availability for flower development (Duchêne *et al.*, 2003).

An alteration of photosynthesis may disturb the whole-plant carbon balance, affecting both reserve restitution (Cruz-Castillo *et al.*, 2010) and carbon nutrition in leaves, flowers, and fruitlets (Berüter and Droz, 1991; Gómez-Cadenas *et al.*, 2000), leading to abscission. Flower and fruit abscission rates appear to be modified when incident radiation (Berüter and Droz, 1991; Aloni *et al.*, 1996; Ferree *et al.*, 2001), leaf area (Gómez-Cadenas *et al.*, 2000; Iglesias *et al.*, 2003; Marcelis *et al.*, 2004), or competition between vegetative and reproductive organs are changed (Smithyman *et al.*, 1998; Vasconcelos and Castagnoli, 2000). These reports suggest that fruit set is linked to assimilate supply (source strength). Further, differences in the ratio of fruitlet abscission between cultivars were highly correlated with the source strength of each cultivar. The importance of leaf photosynthates in fruitlet abscission has also been shown (Gómez-Cadenas *et al.*, 2000). Indeed, in apple, the extent of fruitlet abscission is inversely correlated with the number of leaves on the shoot at the base of the cluster in the spur (Iwanami *et al.*, 2012) and fruit (Atkinson *et al.*, 2002).

## Interaction between carbohydrates and hormones

Carbohydrates and hormones participate in a complex signal transduction system (Gómez-Cadenas *et al.*, 2000). For instance, defoliation treatments at anthesis in citrus induce fruitlet abscission due to a shortage of carbohydrate and a rise in hormones controlling abscission (Gómez-Cadenas *et al.*, 2000; Iglesias *et al.*, 2003). Defoliation reduces sugar concentrations by up to 98%, and raise ABA and ACC levels in fruitlets before their abscission. It was also observed that only the full defoliation treatment reduces endogenous GAs; exogenous application of GAs had no effect on abscission. These results have confirmed the hypothesis that carbon shortage reduces hormonal stimulators of growth (GAs) and increases stress-sensitive signals (ABA and ACC levels) as suggested by Talon *et al.* (1997), who indicated that fruitlet abscission is regulated by ABA and ACC originating in the fruits, while GAs are implicated in maintaining growth. ABA seems to act as a sensor of the intensity of nutrient shortage (higher ABA levels with full defoliation treatment) that modulates the levels of ACC and ethylene, which would be the hormonal effector (Gómez-Cadenas *et al.*, 1996, 1998). ABA is an important signal of water stress; however, in citrus, ABA may be operating as a mediator between the adverse environment and abscission. More recently, Kuang *et al.* (2012) have reported that girdling plus defoliation reduce the endogenous IAA concentration concomitantly with increased fruitlet abscission, highlighting a key role of this hormone in fruit retention.

In tree species, the role of ethylene on the regulation of abscission has been widely illustrated, with this hormone considered as the last hormonal effector of abscission that is induced by different stress conditions (Tudela and Primo-Millo, 1992). The relationship between carbohydrate and ethylene levels in the process of fruitlet abscission has been investigated in citrus (Iglesias *et al.*, 2006). It was reported that ACC treatments, combined or not with sucrose, always increase ethylene production; in contrast, aminoethoxyvinylglycine (AVG) and sucrose reduce the ethylene and ACC. Moreover, branch girdling treatment increases the carbohydrate content and decreases ethylene production, finally decreasing abscission rates (Iglesias *et al.*, 2006; Sun *et al.*, 2010). Finally, a reduction in abscission rate is preceded by elevated concentrations of hexose and starch, but also GAs, in developing ovaries and fruitlets in Satsuma mandarin, suggesting that carbohydrates and GA levels determine fruit set (Mahouachi *et al.*, 2009).

ABA and ethylene appear to act as messengers of auxin in the signalling pathway leading to fruitlet abscission (Agusti *et al.*, 2007b). Reduced supply of auxin to the AZ concurrently with a likely depolarization of its transport would enhance its sensitivity to ethylene and the consequent activation of cell wall-degrading enzymes (Schröder *et al.*, 2013). A transcriptomic analysis has also shown overexpression of a trehalose-6-phosphate synthase gene in abscising fruitlets,



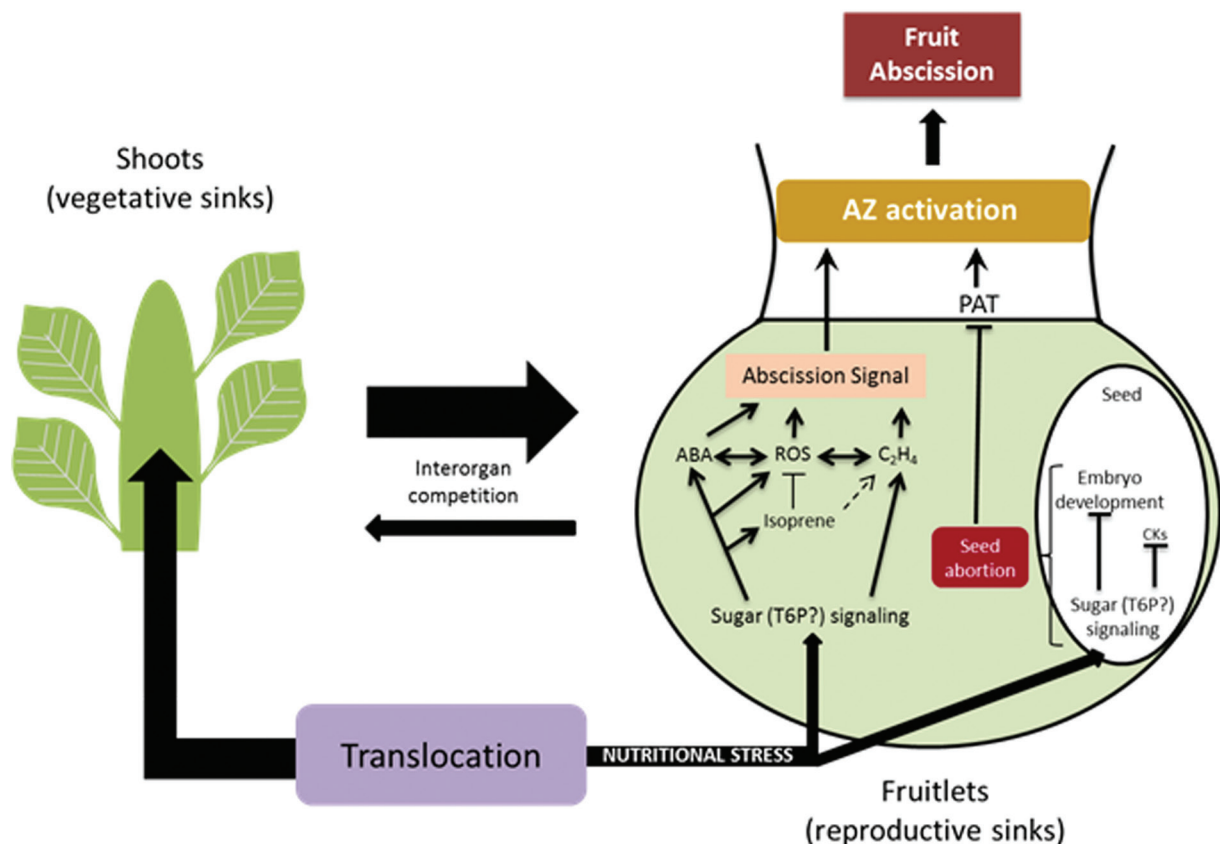
which may regulate ABA signalling in *Arabidopsis* (Avonce *et al.*, 2004).

As auxin plays a pivotal role in plant organ abscission, it is increasingly interesting to investigate the role of genes involved in auxin signal transduction pathways in this process as recently done by Kuang *et al.* in litchi (2012). They reported that under a treatment of girdling with defoliation, expression patterns of many auxin-related genes differ during activation of the fruit AZ.

Eccher *et al.* (2013) have shown a strong correlation in fruitlets between isoprene emission and their abscission potential. Isoprenoid emissions have often been associated with low carbon supply under stress conditions (Loreto and Delfine, 2000; Brilli *et al.*, 2007). Because the oxidative balance in abscising fruitlets is disrupted by high levels of ROS, isoprene might act directly to ROS accumulated in the fruit cortex (Velikova *et al.*, 2004; Vickers *et al.*, 2009; Botton *et al.*, 2011). Therefore, the fruit stimulated to abscise may exploit isoprene emissions to recover a noncytotoxic oxidative status using a nonenzymatic ROS-scavenging system (Eccher *et al.*, 2013). Exogenous application of ABA to apple is able to magnify fruitlet abscission but not to affect

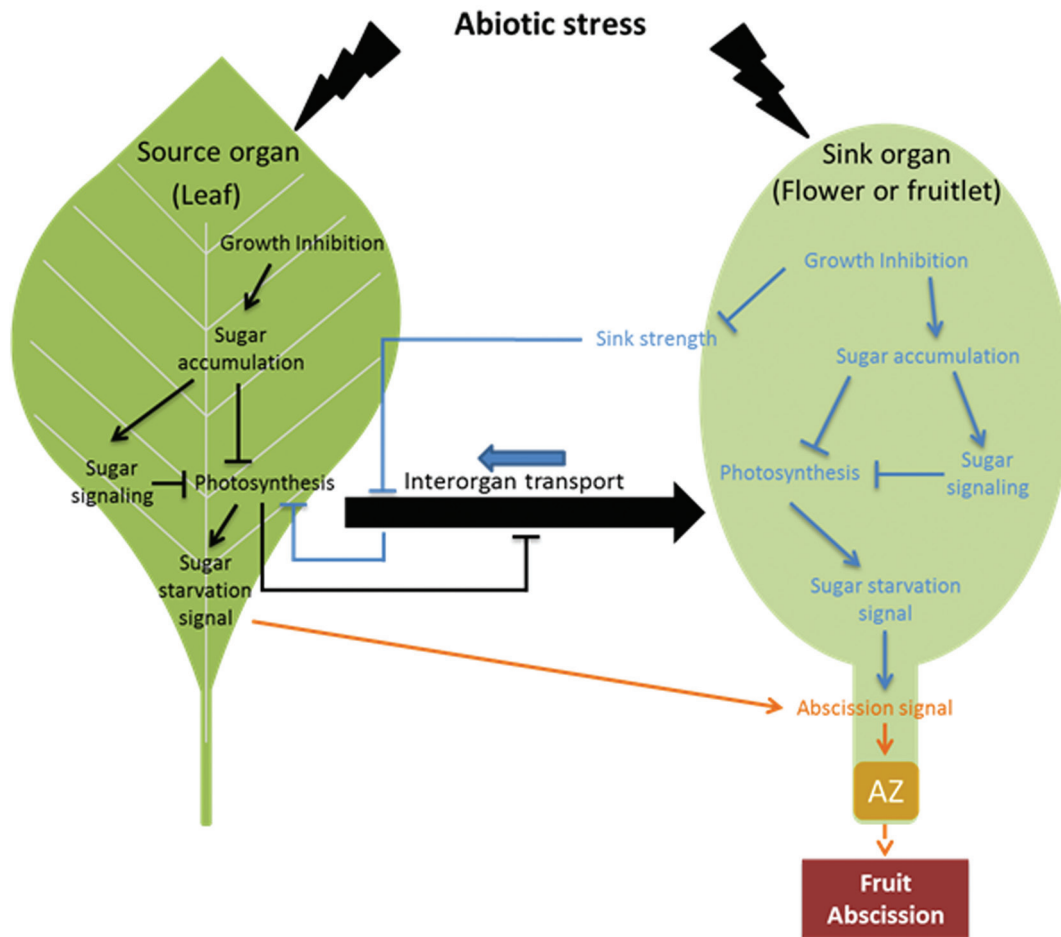
isoprene emission (Eccher *et al.*, 2013). Thus, the involvement of ABA seems to be upstream of abscission induction and not a side effect of this process. Multiple networks of interaction between hormones (mainly ABA and ethylene) and other signalling molecules (i.e. ROS) orchestrate the abscission process at the cortex level. During induction of abscission, the production of both isoprene and ABA appears to be temporally coordinated, with a potential isoprene involvement in the ROS detoxification and activation of still-unknown secondary signalling pathways.

By adding together the results reported by Botton *et al.* (2011) and Eccher *et al.* (2013), an updated model of the induction of abscission under nutritional stress has been proposed (Fig. 4). Although this hypothetical model must be validated, we may hypothesize that under abiotic stresses, which lead to alterations of carbohydrate metabolism and therefore to nutritional stress, the same processes might occur, leading to abscission. This model may also have future applications, notably for the characterization of flower abscission, since abiotic stresses lead to alterations of flower development, pollination, and fertilization, which are also highly regulated by hormones.



**Fig. 4.** Hypothetical model for fruitlet abscission under nutritional stress [according to Botton *et al.* (2011) and Eccher *et al.* (2013)]. The nutritional stress, enhancing the competition for assimilates between vegetative and reproductive sinks, is translated at both the fruit and seed levels through crosstalk between signalling pathways involving mainly sugars, ABA, and ethylene. Sugar signalling includes processes of sugar starvation, growth inhibition, sucrose accumulation, and trehalose-6-phosphate (T6P) signalling as described by Botton *et al.* (2011). In the fruit, the sugar signalling (through T6P) induces ABA and ethylene synthesis, which can increase ROS content and lead to an abscission signal. The abscission signal is then transmitted to the AZ, leading to fruit fall. When the seed perceives sugar depletion, a block of embryo development and cytokinin (CK) signalling occurs, leading to seed abortion. This crucial step would determine the depolarization of auxin transport, leading to the enhancement of AZ sensitivity to ethylene and its activation. The thickness of the arrows related to interorgan competition and storage partitioning is proportional to the strength of the organ as a sink.





**Fig. 5.** Schematic representation of flower/fruitlet abscission following exposure of leaf or flower to abiotic stress. In the leaf, to abiotic stress inhibits development and decreases photosynthesis, leading to sugar starvation, perceived as unrecoverable by the fruit, which aborts. In flowers or fruitlets, the stress affects growth and photosynthesis. Consequently, the sugar balance between leaf and flower is altered and nutritional stress occurs. The sugar depletion induces an abscission signal leading to flower/fruit fall. Black arrows, leaf process; blue arrows, flower/fruit process; orange arrows, common process.

## Conclusions

Environmental stresses, leading to physiological perturbation in plants, extensively increase abscission and lead to important yield decreases. Hormones mediate the response of organs (flowers or fruits) to stress and finally trigger abscission. Hormones are the abscission effectors since they modulate AZ activation within a complex signalling system based on synthesis, catabolism, and transport of hormones. The auxin/ethylene balance is of a particular importance due to its action on AZ sensitivity and activation. Carbohydrates also participate with hormones in a complex signal transduction system in response to stress, leading to abscission.

Since abiotic stresses lead to an imbalance of carbon between source and sink organs (Fig. 5) and therefore alter the nutritional equilibrium at the whole-plant level, future experiments should target the relationships between the source and sink organs using photosynthesis inhibitors. Understanding how distinct reproductive organs cope with stress might offer the potential to identify new traits that could be manipulated to improve their stress tolerance. Elaboration of models should allow the development of new

strategies to improve stress tolerance, notably with the use of polyamines and brassinosteroids, implied to be involved in the abiotic stress response by stimulation of the carbon status. Transcriptomic, metabolic, and hormonometric analysis should be developed in woody species during flower and fruit development in order to strengthen models in different crop systems to increase resilience to environmental stresses while preserving productivity and quality.

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