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Fruit drop: II. Biological background of flower and fruit drop

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Summary: The most important components of fruit drop are: the rootstock, the combination of polliniser varieties, the conditions depending of nutrition, the extent and timing of the administration of fertilisers, the moments of water stress and the timing of agrotechnical interventions. Further adversities may appear as flushes of heat and drought, the rainy spring weather during the blooming period as well as the excessive hot, cool or windy weather impairing pollination, moreover, the appearance of diseases and pests all influence the fate of flowers of growing and become ripe fruits. As generally maintained, dry springs are causing severe fruit drop.

In analysing the endogenous and environmental causes of drop of the generative organs (flowers and fruits), the model of leaf abscission has been used, as a study of the excised, well defined abscission zone (AZ) seemed to be an adequate approach to the question. Comparing the effects active in the abscission of fruit with those of the excised leaf stem differences are observed as well as analogies between the anatomy and the accumulation of ethylene in the respective abscission tissues.

Key words: fruit drop, abscission zone (AZ), physiological bases, hormonal bases, structural biology, molecular biology

Physiological and hormonal bases

As a consequence of fertilisation – in most cases immediately after pollination – the ovary starts intense growth, i.e. this is the beginning of fruit growth. Meanwhile, the petals, stamina and stigmata as parts of the perianth start fading and abscise. The early changes of the flower after a successful fertilisation are the signs of fruit set (*Pethő,* 1993). In some cases, the mere fact of pollination may also initiate the growth of the ovary. Without fertilisation, the degeneration of the ovary is expected, which is followed by the death and abscission of the flower too. Flower drop is caused according to *Szalai* (1994) by the appearance of ethylene-produced auto catalytically. The same phenomenon is experienced in fruit species with unisexual flowers (e.g. walnut), where the male flowers fade (get senescent) immediately after the release of pollen grains. The peculiar phenomenon of the abortion of female walnut flowers has been attributed to an excessive amount of pollen sticking to the stigmata, where ethylene is produced (*Soltész et al.,* 2003).

As a rule, the pollinated flower will develop to a fruit, and the fertilised ovules grow to seeds due to an intense synthesis of growth substances. They appear first in the developing endosperm of the seed primordia (ovules) and penetrate the wall of ovary (the future pericarp) as well as the other parts of the fruit primordium including the peduncle. The centre of organic synthesis of the fruit primordium keeps being the growing embryo and the surrounding endosperm. The intense cell division and growth of the tissues absorbs a lot of organic matter of the reserves competing with the vegetative organs, consequently, an interaction between the different parts of the organs of the tree is building up. Not only the fate of the growing fruit, its size and quality but also the physiological potential of the whole tree is influenced by relations of sources and sinks, which in turn may impair the maintenance of the fruits set. The growth substances (auxins and gibberellins) induce the growth and thickening of the peduncle too. (*Tari,* 2004c) This process needs much organic substance, which may prove to be insufficient and the response of the organism is expressed in the abscission of a fraction of the developing fruits.

Following the flower drop, fruit drop ensuing before maturity is attributed to the collapse of the "hormonal balance" in the growing fruits, where the growth substances being active in favour of growth (auxins, cytokinins, gibberellins) lost their influence against abscisic acid (ABA) causing abscission. *Davis & Addicott* (1972) were the first in proving the role of ABA, which became prevalent when the young fruitlets dropped, and a second maximum has been observed, when fruits are almost ripe. The difference between varieties prone to fruit drop corresponded to their ABA content too.

Recently, some students came to the conviction that the correlation between endogenous ABA content and fruit drop is not immediate. Milborrow (1974) reported in his detailed study that among a couple of hundred plants sprayed with ABA in several cases the expected response was not observed, surprisingly, no abscission occurred.

Natural fruit drop and production of auxin was another aspect of the same question (*Soltész*, 2002), the abscission of young fruits seems to depend on auxin as a correlative dominance signal (*Bangerth*, 1990). The investigations of *Luckwill* (1948, 1953a, 1953b) are decisive in searching the causal relations between auxin production of the developing fruit and fruit drop *(Figure 1). Abeles & Rubinstein* (1964) also found an explanation, how IAA may speed up or alternatively inhibit the process of abscission.

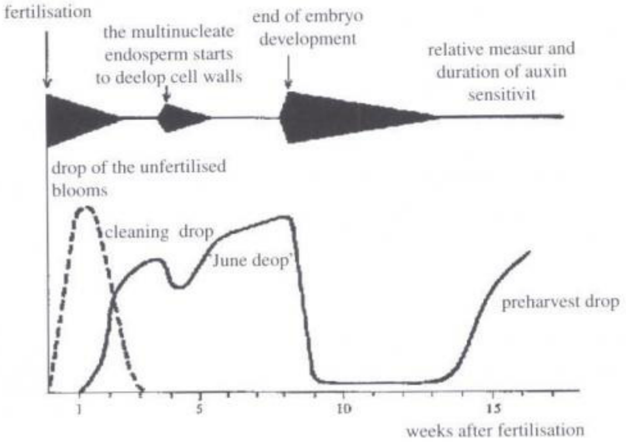

Figure 1. Relationship between hormonal activity and fruit drop in apple (after Luckwill, 1953)

The endosperm of the ovule (seed primordium) is the source of auxin production. Most intense activity is observed at the time from fertilisation and the start of embryo development. The auxins produced are flowing through the peduncle of the fruit into its basis where the rudiment of the abscission tissue is located and inhibit the development of corky walls. The flow of growth substances does not exist at the basis of unfertilised flowers; therefore they abscise soon (*Friedrich*, 2000).

In young fruits, the level of auxin content is closely dependent on the binding of the free IAA to amino acids, as IAA-Asp and IAA-Glu (*Slovin & Cohen*, 1993). It is supposed to be essential from the point of view of fruit drop.

According to *Bubán* (2003), the premature abscission of fruits is determined by the relative concentrations of IAA and ABA. After bloom, the level of ABA (*Talon et al.*, 1990a), or of the ratio ABA/IAA is increasing the frequency of abscission (*Brummett*, 1988). The role of ABA in abscission has been proved in apple (*Vernieri et al.*, 1992), litchi (*Yuan & Huang*, 1988), citrus (*Talon et al.*, 1990b; *Sagee & Erner*, 1991; *Goren*, 1993; *Gomez-Cadenas et al.*, 2000) as well as in cotton (*Guinn & Brummett*, 1988). The increasing ABA level is caused most likely as a reaction to any kind of stress condition (drought, troubles of nutrient supply, etc.). *Pozo* (2001) showed the combined role of ABA and of inhibiting compounds like jasmonic acid in the development of abscission tissue of citrus fruits as a complex signal of fruit drop. Also *Tari* (2004b) proves the presence of jasmonic acid in abscission.

Several authors have confirmed the important role of ethylene in fruit drop. *Tari* (2004a) maintains that the principal regulator of abscission is ethylene, which is suppressed essentially by IAA. Ethylene causes the abscission by dissolving the middle lamella of cells and the cell walls are hydrolysed in the abscisic tissue at the basis of the peduncle (fruit stem). It is proved that ethylene stimulates the *de novo* synthesis pf the enzyme cellulase and its action on the cell wall (*Abeles*, 1973). The target cells of ethylene effect are those of the abscisic tissue. The cells of a narrow layer increase in size (and become soft), locally, by the action of IAA and separate the fruit basis by a kind of shearing effect.

Abeles (1973) as well as *Abeles & Leather* (1971) concluded that fruit drop is not the result of ethylene formation but rather of the increasing susceptibility towards ethylene of the respective cell layer (the abscisic tissue used to consist of 2–5 layers). Jackson & Osborne (1970) found an increasing level of ethylene content anticipated that natural abscission.

During the years of the late 1970-es, several students attempted analysis of the substances stimulating the abscission process and stated the presence of other substances than ABA as xanthoxin and another, which could not be identified yet (*Szalai*, 1994).

Behind the hormonal background of premature fruit drop there are – among others – causes like lack of nutrients, which does not depend solely on the meagre soil, but rather on the competition between the vegetative organs and the growing fruits of the plant. The fate of a young fruit is often impaired by the dominance of another fruit or vigorous shoot(s). On the contrary, a physiological process of senescence more likely sheds the fruits near to maturity.

The abscission of young fruits and fruit primordia is caused by the regime of quite different phenomena than the drop of mature fruits (*Bubán*, 2003). In the latter case, the ripening of fruits is preceding the abscission. *Osborne* (1979) for instance – debated by other students – represents the supposition that senescence gives the triggering signal to the abscission process. Many data argue that the distal tissues do not senesce before the process of abscission under normal conditions, and all the same, fruits are dropped often far from being ripe. Senescence and abscission, though appearing together, are not connected always as cause and consequence, and may ensue sometimes independently (*Szalai*, 1994).

According to the above arguments we should distinguish three types in the drop of generative organs:

1 Caused by the lack of fertilisation, the flowers are shed, and rate of the fruit set will be low. Its mechanism was amply treated above.

2 Abscission of young, developing fruit primordia, which may divide into several periods, but never related to the natural processes of senescence.

3 Natural drop physiologically ripe or nearly ripe fruits, which is related to some kind of senescence. Practically, its significance is minor in fruit growing.

As explained earlier, not all fruits set during the blooming period will attain full maturity because of being abscised prematurely. Frit drop is essentially the expression of a kind of autoregulation mechanism in plants (*Andrássy*, 2004), which restores the physiological balance of the tree (*Szalai*, 2005). The natural fruit thinning is a conditional trait of fruit plants, which is a component of the strategy of the living organism, which is aimed to secure the maximum of yield in each phase of the growing cycle: number of generative organs, bloom, fruit set, number of fruits with viable seeds. The striving for the possibly highest number of progeny is the basis of exploiting the performance of cultivated plants (*Stösser*, 2002). The autoregulation of the plants serves the same purpose by securing the development of those fruits, which contain more viable seeds, whereas the less productive ones are dropped in favour of those, which are more productive.

Summing up the aspects of fruit drop, we state the most important components: the rootstock, the combination of polliniser varieties, the conditions depending of nutrition, the extent and timing of the administration of fertilisers, the moments of water stress and the timing of agrotechnical interventions. Further adversities may appear as flushes of heat and drought, the rainy spring weather during the blooming period as well as the excessive hot, cool or windy weather impairing pollination, moreover, the appearance of diseases and pests all influence the fate of flowers of growing and become ripe fruits. As generally maintained, dry springs are causing severe fruit drop (*Molnár*, 2004b).

Fruits, which abscised prematurely continue their life, but never attain true maturity because of abnormal biochemical processes, which cannot be changed during after-ripening procedures and remain defective also in taste and colour. This is referring mainly to pomaceous fruit species.

Preliminaries of structure and of molecular biology

In analysing the endogenous and environmental causes of drop of the generative organs (flowers and fruits), the model of leaf abscission has been used, as a study of the excised, well defined abscission zone (AZ) seemed to be an adequate approach to the question. Comparing the effects active in the abscission of fruit with those of the excised leaf stem differences are observed as well as analogies between the anatomy and the accumulation of ethylene in the respective abscission tissues (*Dávid*, 1980).

The abscission of fruits is generally coupled with structural changes in the plant (*Baird & Webster*, 1996), which means that several abscission zones (AZs) are formed within the same inflorescence. *Fehér* (1925) postulated the possibility of the appearance of two or three AZs around the same fruit. In sweet cherry e.g. the first zone is formed at basis of the fruit, the second at basis of the peduncle, whereas a third one at the basis of the inflorescence. (*Bradbury*, 1929; *Stösser et al.*, 1969a, 1969b; *Bukovac*, 1971).

In leaf stem, cell division starts at a well-defined region before the abscission (i.e. secession of cells) ensues. In flowers and fruits, however, no cell division took place; furthermore, neither a definitive layer of abscission was formed. In the AZ of most fruits, the separation of cells shows an irregular pattern in a region of parenchymatous cells on the border of supporting tissues (*Stösser* et al., 1969b; *Wittenbach & Bukovac*, 1972). The separation ensues between cells, where the middle lamella became soft by the action of hydrolysing enzymes (*Szalai*, 1994).

Fruits are abscised because the cells got loose in the AZ. Pectin, hemicelluloses and cellulose are dissolved by the respective enzymes, and the mechanical stress detached the fruit. Sometimes, the dead xylem elements keep the fruit hanging a while (*Szalai*, 1994). As external agents, the wind may help the drop, but the dehydration of senescent cells causes tension and contributes to the process. The scar of the detached fruit is generally suberised or lignified (*Haraszty*, 1978).

The process of abscission is more comprehensible if the biochemical background was cleared. By all one or two cell layers are involved, where the separation takes place. The biochemical regulation should be explored there. In the abscission fruits, not the whole AZ of the peduncle is involved, but at the distal end a layer of 1–5 cells, which is called the layer of separation. Those cells are small, iso-diametric, their cytoplasm is dense, their intercellular space is narrow, contain much starch, and are connected with many plasmodesmata (*Tari*, 2004c).

Anatomic investigations in apple, sweet cherry and peach prove that the AZ is genuinely distinct from the surrounding tissues, not only after activation of the process of abscission (*Stösser et al.*, 1969; *Bargioni & Ramina*, 1972; *Rascio et al.*, 1985; *Pandita & Jindal*, 1991; *Costa et al.*, 2005). The AZ of apricot has been studied by Robbins (1931), *Robbins & Ramaley* (1933), intrinsically. The scars of the perianth and the style are similar to that of the peach, and the whole blooming process and abscission has been divided into 10 periods by *Lott & Simons* (1968).

The AZ is distinct from the rest of tissues not only in its anatomy but also in metabolic terms. AZ excels by intense cell division, synthesis of proteins and RNA, high O_2 consumption as well as peroxidase-activity. Important role is attributed to the middle lamella and the attached primary cell wall, as being dissolved. The middle lamella is softened by the enzyme pectin-esterase, which demethylate the pectin making it soluble and the cells are easily separated. Another enzyme, cellulase is also activated together with galacturonase (*Szabó*, 2004).

During the course of abscission, the AZ initiates the jamming of the xylem elements inhibiting the metabolic transport to the fruit. In the xylem, a polysaccharide, the tylose intrudes from the parenchymatous cells and makes burst the transporting cells. The xylem starts splitting along the middle lamellae leaving the cells unimpaired. The phloem is barred most likely by callose, another polysaccharide. The activity of the AZ is building up a physiological dike against the further spread of the process of senescence (*Szabó,* 2004).

Abscission at the AZ is genetically fixed and typical for the respective species. The size of cells is smaller than in the neighbouring tissues. The expansion of those cells is delayed and their meristematic character maintained. It is supposed that the susceptibility of the respective cells to the "signal of abscission" is held open by that way (*Szalai,* 1994).

The first sign of the AZ cells is the lag of the cycle, when the cytoplasm became dense and its organelles accumulate. Especially the Golgi-apparatuses and the endoplasmic reticulum are appearing more conspicuous. At the same time, a revival of the intensity of respiration and synthesis of RNA and proteins is states. In this phase, the process of abscission is easily slowed down by the inhibition of respiration as well as by the synthesis of RNA.

Approaching the end of the lag-phase, the histochemical character of the respective cells is also recognised. The nuclei of those cells are large and the autoradiographic measurements prove the intense RNA and protein synthesis. The ultrastructural pictures show the separation along the middle lamella, and the integrity of the cells at the line of dehiscence.

The biochemical process of the dissolution of the cell walls is also supported by the fact that in the AZ, the cells are different in the respect of their chemical composition. Our present knowledge suggests the existence of a "hidden" differentiated cell layer, which was called by Osborne (1979) as "target cells". That type of target cells occurs also in other parts of the plant, e.g. the resin ducts, aerenchym, lenticels, where the cells are similar to the cells of the AZ.

The physiological processes of abscission are divided into two qualitatively distinct phases (*Tari,* 2004a):

I. The phase of maintenance of the fruit
II. The induction of abscission (when the signal of abscission arrives and the transfer of the signal ensues and meanwhile the synthesis of growth substances increases) subsequently the separation starts.

In the Ist stage, auxins inhibit the abscission by the repression of the synthesis of hydrolytic enzymes. It is generally known since long that the isolation of the source of auxin synthesis stimulates the abscission and the exogenous auxin administered inhibited the abscission.

The abscission is delayed or even stimulated by auxin (IAA) depending on the site, where the agent is applied, i.e. distally or proximally to the AZ. That phenomenon was explained according to the gradient of the "Addicott gradient", which stated that higher concentration of IAA applied on the proximal side of the AZ accelerates the abscission, on the distal side inhibits it (*Szalai,* 1994).

The IInd stage begins with the moment when auxins loose their inhibitory effect. As for the mechanism, it is highly probable that the auxin-binding capacity of the tissues is responsible, in other words, by the regression of auxin-binding sites of the special membranes in the AZ, the growth substance looses its capacity to act. At the same time, the proton-extrusion caused by auxin diminishes. It means that auxin binding and proton-extrusion are decisive moments of the process. Further proofs seem to be the fact that fusicoxin causing proton-extrusion too delays the abscission already during the Ist stage.

In the IInd stage, ethylene plays an important role. As the level of auxin diminishes, the level of ethylene increases. Ethylene – as explained in the former chapter – reduces the synthesis of auxin and inhibits the transport of in from the fruit into the peduncle, moreover, accelerates the enzymatic dissolution of the cells. The diminishing concentration of free auxin increases the susceptibility of the target cells to ethylene. The target cells of AZ synthesise the enzyme cellulase.

Ethylene exerts a positive effect on *de novo* synthesis of cellulase, and activates also other enzymes. A proof of it is also actinomycin-D, which restrains the abscission mainly during the early part of the IInd stage. The inhibitory agents of ethylene as CO_2 and Ag^+ also delay abscission. As indicated earlier, ABA is also stimulating abscission. It restrains the transport of IAA, but does not shorten the length of the Ist stage. It has, most likely, special influence on the enzymes dissolving the cells or on the formation of ethylene.

The ion Ca^{++} too is active in the regulation of abscission. There is a loss of Ca^{++} in the cell walls experienced in abscission, and an administration of Ca^{++} into the AZ restrains the process of abscission.

During the phase of abscission, the genes responsible for inducing the synthesis of hydrolytic enzymes dissolving polysaccharides of the cell wall mainly as cellulases and pectinases are activated. Those enzymes dissolve the middle lamella and also the cell walls and the cohesion of cells is weakened. An abscission-specific cellulase (e.g. 9.5 cellulase) and a non-specific (e.g. 4.5 cellulase) are distinguished according their different iso-electric points. The expression of the abscission-specific cellulase is inhibited specifically by norbornadiene, which restrains the binding of ethylene to the receptor. The presence of the mRNA of the cellulase could be detected in 2–2 cell layers on the both sides of the line of abscission. Meanwhile in the abscission layer, enzymes and proteins are induced, which are involved in defence reactions to pathogenes and pests, e.g. chitinases and ß-1,3-glucanases (*Tari,* 2004a).

It has been detected that the drop of fruit primordia in apple could be associated with the rising level of transcripts of the *MdACS5B* gene (*Dal Cin et al.,* 2005, in: *Costa et al.,* 2005). Following the signal induced abscission; 8 days elapsed, when the differences could be detected between the fruitlets to be shed (AF) and the non-abscising ones (NAF). On the contrary, in the fruit stems of AFs an accumulation of transcripts was found already at the 6th day and it continued until the 12th day at the end of the experiment. In the fruit flesh as well as in the AZ too, the transcripts accumulated quickly during the process of abscission. The gene *MdACO2* was expressed on higher level than the *MdACS5B*. In all tissues examined, there was an accumulation of transcripts.

The most accumulation was found in the seeds during the experiment. The transcripts of the AZ and of the fruit stem appeared already at the 4th day and kept the high level continuously. The changes described were similar also in the fruit flesh as in the AZ and fruit stem, but an outstanding rise was experienced at the 4th day *(Figure 2)*.

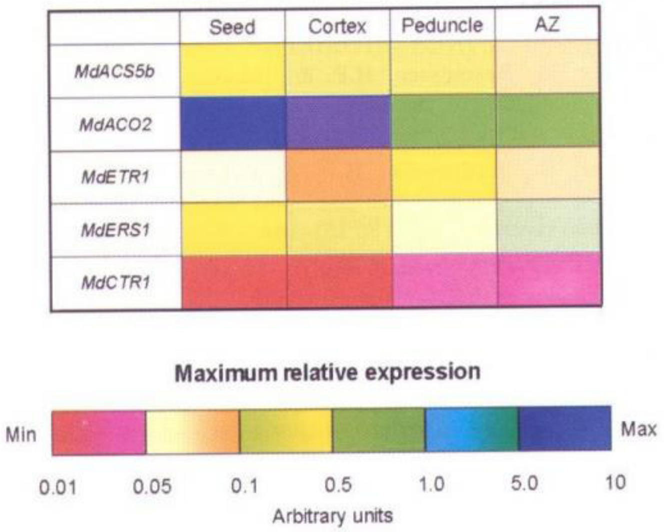

Figure 2. Expression of apple genes involved in ethylene biosynthesis (*MdACS5B*, *MdACO2*), perception (*MdETR1* and *MdERS1*) and signal transduction (*MdCTR1*) in seed, cortex, peduncle and AZ at early fruit development stage (Costa et al., 2005)

The specificity of AZ is connected to the susceptibility of tissues to the induction of abscission, especially to ethylene.

The ETR1 is coding a protein, which is similar to a bacterial regulator of two components and contains the same set of amino acids (Ecker, 1995). The CTR1 is another gene like the Raf kinases from the point of view of its amino acid composition, and is supposed to perform a negative regulation of the signal of photophosphorylation (Kieber, 1997). Recently, the ethylene receptor ETRI of *Arabidopsis* was compared with its homologues derived from peach (Tonutti et al., 1997) as well as apple (Dal Cin et al., 2005) and its expression was checked on the AZ of the fruit species mentioned. The level of transcripts of *Md-ETR1* and *Pp-ETR1* was nearly invariable during the process of abscission, however, only the quantity of mRNA of *Md-ERS1* and *Pp-ERS1* increased during the activation of abscission in the AZ. Seemingly, the *ETR1* was expressed structurally (Tonutti et al., 1999), whereas *ERS1* was overregulated by ethylene, which may be related to abscission (Rasori et al., 2002; Dal Cin et al., 2005) *(Figure 3)*.

Aknowledgement

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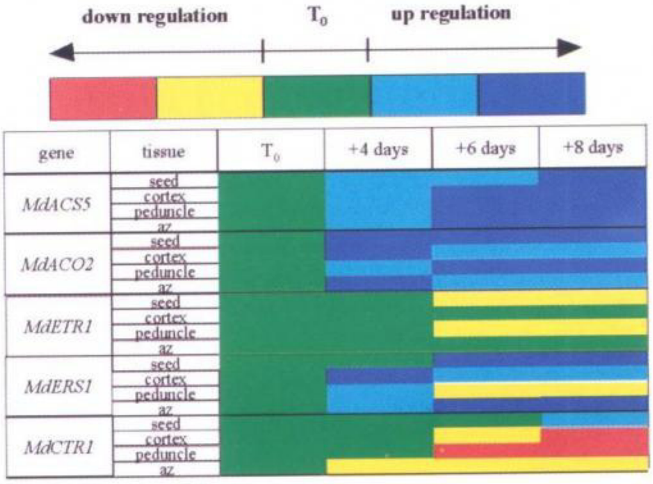

Figure 3. Relative expression of genes involved in ethylene biosynthesis (*MdACS5B*, *MdACO2*), perception (*MdETR1* and *MdERS1*) and signal transduction (*MdCTR1*) in seed, cortex, peduncle and AZ throughout the activation of abscission of fruitlet abscission. The original expression of different genes was equalized at the time 0 (T_0= green). Down- and up-regulations are represented by an arbitrary color scale (dark blue = maximum up-regulation; red = maximum down-regulation). (Costa et al., 2005)

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