Invited lecture

PHOTOSYNTHESIS INHIBITION AS A TOOL FOR APPLE FRUITLET THINNING

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Abstract. The possible mechanisms of apple fruitlet abscission are presented in this paper. Prevailing hypothesis on hormonal triggered processes in the event of "correlative dominance effects" of adjacent fruitlets or nearby shoot tips has the opponent theory of assimilate supply dependent fruitlet abscission. Assimilation shortage may also be involved in the correlative auxin processes but the connections of both statements are not clear yet. On last years a lot of evidence is provided in support of assimilation dependent fruitlet abscission process. At the time just after the end of the flowering, a strong competition between fruitlets and shoots for photosynthates exist. Shading experiments comparable for a few days of cloudy weather provoked strong natural apple fruitlet abscission. If the applications of chemical thinners are followed by a few days of shading, much stronger abscission occurs comparing to thinner applications without shade. A photosynthesis inhibitor metamitron has gone into registration for fruitlet thinning purpose and is available in Europe last year. A good thinning results can be achieved up to 14 mm king fruit diameter, but additional studies should be made to adapt dosage for the present and predicted light intensity at the time just after metamitron application.

Keywords: apple fruit, shading, metamitron, thinning agents, photosynthesis.

Introduction

Apple production is based on regular, annual crops of high internal and external fruit quality. Frequently, apple fruit trees form too many flowers and set too many fruit to obtain high quality and regular marketable crops throughout the year. The main problem of too high fruit set is abundant yield of low quality fruits. Secondly, one of the biggest problems of high yielding apple and pear orchards is alternate bearing phenomenon. A prerequisite for an annual crop is an adequate initiation of flower bud formation, which can only be achieved when there are not too many fruitlets per tree. The chemical thinning of flowers or fruitlets is actually the only way to avoid alternate bearing and to improve fruit appearance. Thinning of flowers or fruitlets improves fruit appearance and return bloom and has become a standard practice in the growing of many fruit crops (Greene and Costa, 2013). Chemical thinning has been regarded as the most satisfactory method of thinning since it is the most cost-effective and it is relatively fast so it can be done at critical times and has the greatest positive effect on return bloom. For this reason, the chemical thinning practice has been customary in intensive apple production for 40 years and more (Costa *et al*., 2005).

Several chemical thinners are currently available, but not all may remain on the market or be used in specific circumstances. Basically two approaches to fruit set reduction are used: flower thinning and fruitlet thinning. Flower thinning is not popular with growers, because they are reluctant to eliminate a proportion of the flowers prior to ensuring adequate fruit set. However, in the case of cultivars that annually set abundantly or in the case of favourable climatic conditions for fruit set, flower thinning is the standard practice. In this case later fruitlet thinning is insufficient to reduce fruit set adequately (Wertheim and Webster, 2005). Chemical flower thinning is performed with caustic compounds which make the injury to the generative organs in the flowers (also are called pollinicides). One of the first flowers thinner was sodium-dinitro-ortho cresylate (DNOC) which remained an important blossom thinner for arid regions until 1990 when registration ceased. After then wide search for the new bloom thinners has been activated and continuous even today. In Europe ammonium thiosulphate (ATS) is the most evaluated and used blossom thinning agent on apples. Beside ATS, hydrogen cyanamide (Dormex), endothalic acid (Endothal) or sulfcarbamide (Wilthin) were more or less successfully used on apples or on stone fruit (Fallahi *et al*., 1998; Fallahi and Williemsen, 2002). Many other desiccating chemicals have been researched but most have been unsuccessful because of lack of thinning at low concentration or phytotoxic side effect at higher concentration. Lime sulphur, sodium chloride, potassium bicarbonate and fish or plant oils was found to effectively thinned apples if applied to full bloom at concentration lower than 3% (Bound, 2010; Stopar, 2004).

Much more interesting for the growers is the use of fruitlet thinners. They can be used from post-bloom period up to 20 mm fruitlet diameter. In the world market we could find following traditional apple fruitlet thinning compounds: naphthaleneacetamid (NAD), 1-naphthaleneacetic acid (NAA), ethephon, 6-benzyladenine (BA) and carbaryl. In the last year’s carbaryl disappeared from many countries, including all European states, because of ecological and toxicological reasons, high persistency and toxicity for the bees. The main problem of all these compounds is the inconsistency of the thinning action and/or unpredictable thinning results. Beside tree condition (age, vigour, bloom density, stress, etc.) and cultivar characteristics, weather condition can strongly affect thinning response of individual tree (Dennis, 2000; Wertheim and Webster, 2005; Williams, 1994). Also some negative effects of thinners on fruit size were found. Higher concentration of NAA may over-thin or reduce fruit size on some cultivars as ‘Delicious’ or ‘Fuji’, or not increase fruit size even though crop load is substantially reduced (Stopar and Tojnko, 2005). NAD should not be used on ‘Delicious’ because of high percentage of pygmy fruit can happen (Williams and Edgerton, 1981). Pygmy fruit can be the result when NAA + BA are combined for thinning some apple cultivars as ‘Delicious’ (Bukovac *et al*., 1994). These are the reasons for searching the new thinning compounds. Thinning properties of abscisic acid (ABA) was proved on apples and pears and the most effective time of application was found at 10 mm fruitlet diameter (Greene *et al*., 2011). Aminocyclopropane-1-carboxylic acid (ACC) is the new, promising but not yet registered thinning agent (Greene and Costa, 2013). The new thinning agent already registered on all European countries and waiting for registration in US is the photosynthetic inhibitor metamitron. Metamitron has been reported to be quite active as a thinning agent for pome-fruits, mainly for apple and pear (McArtney and Obermiller, 2012).

The theory of apple fruitlet abscission

Shortly after flowering non-pollinated or non-fertilized ovaries, which were grown only minimally, are shed in the so called "first drop". A week or two later the second drop start to begin and this drop is called "June drop". Second drop can be done in one or more waves, mostly at about 8-12 mm fruitlet diameter (middle of May), and after that, not necessarily, in the start of June or later to the end of June. The last theoretically distinctive drop is the drop of fruit before harvest, where the premature full-grown fruit shed in so called "preharvest drop".

In the case of leaves the abscission is an event repressed by auxin and activated by ethylene or is controlled by an "auxin-ethylene balance", i.e. the relative concentrations of auxin and ethylene in the abscission zone determine to which side the balance between abscission or retention tips (Osborne, 1989; Sexton, 1997). If tips towards the ethylene side, the cell-wall break down in the leaf petiole abscission layer occurs and abscission follows. If the balance tips towards the auxin side, no breakdown or abscission of leaves occurs. Senescence, darkness, drought, wounding and the presence of abscisic acid increase the ethylene supply. Some of these factors reduce auxin supply as well such as low light conditions or wounding. Active growth is the main factors which increase auxin supply (Tromp and Wertheim, 2005).

The drop of young fruitlets is more complicated than the described above for the leaves, and is so called "correlatively triggered" abscission. According to this hypothesis, put forward by Bangerth (2000), young fruitlets senescence only starts after their drop is already decided by a correlative event. In fruitlets that are destined to shed, auxin export seems to have been reduced to a lower level by "correlative dominance effects" of adjacent fruitlets or nearby shoot tips. In the phenomenon called "primigenic dominance" the fruitlet which set first dominate above later set fruitlets (Bangerth, 1989). Fruitlets which set later (the dominated fruitlets) or the fruitlets near the growing shoot tips show a lower auxin export and a reduced growth rate. The explanation is that although dominating or dominated fruitlets and shoot tips all export auxins, at junctions where the auxin streams meet, the stronger polar auxin transport (mostly from dominating fruitlet or shoot tip) inhibits weaker one (from dominated organs). This causes an auto-inhibition of auxin production in the dominated organs. Possibly the cytokinin synthesis of the dominated fruitlet is reduced as well, which would further affect fruitlet growth negatively. The overall result is that the auxin transport through the abscission zones of many weak fruitlets is increasingly reduced until a point at which abscission is inevitable. Ethylene is needed for the final step in this process, the induction of necessary enzymes for cell-wall break down. Also should be noted that polar auxin transport from a fruitlet is essential for an adequate vascular tissue differentiation in pedicel. A good vascular connection allows adequate supply of water, minerals and assimilates to the fruit, and also allows further polar auxin transport itself, by feedback auxins stimulates its own transport, synthesis and/or concentrations. Moreover, organs with a high auxin-diffusion rate have a direct attractive effect on assimilation transport (Bangerth, 1989).

The dominance of one fruitlet over another depends on time of fruitlet set, on seed number and number of fruitlets per cluster. The first set fruitlet, also in the dominant position in the flower cluster (known as king fruit), show stronger auxin transport comparing to lateral set fruitlets. The dominance of shoot tips over neighbouring fruitlets in the cluster depends of their proximity and vigour (Tromp and Wertheim, 2005).

Assimilation shortage may also be involved in the correlative auxin processes. It has been observed that NAA, NAAm or ethephon reduce leaf net-photosynthesis, just at a time when leaf area is small and fruitlets and shoots growing away rapidly. The combination of a reduced auxin transport from dominated fruitlets by correlative inhibition plus assimilates deficiencies leads to the formation of stress ethylene, which in turns induces abscission (Untiedt and Blanke, 2001). Further, some fruit growing practices as girdling, using growth retardants or dwarfing rootstock, bending of shots reduce the degree of fruitlet shedding, and at the same time reduce shoot growth. Retarded shoots have more surplus of assimilates and lack of competition for carbohydrates do not push fruitlets into abscission – is one story. Also at the same time retarded shoot do no export a lot of auxins from growing tips (which stop to grow) and would not present dominating auxin streams from shoot tips, and fruitlets would persist in the cluster – is the second story. Both stories can be coupled by correlative inhibition effect where auxin export is the primary signal, but it is difficult to completely rule out temporary carbohydrate shortage as a main (independent) factor of fruitlet abscission.

Possible mode of action of main thinning agents

Most thinning agents are effective only when applied prior to the period of June drop, when fruitlets abscission is occurring spontaneously. Fruitlet abscission is not accompanied with leaf abscission, nor do thinning agents induce leaf abscission when applied at this time. These facts suggest that chemicals only stimulate the process of natural abscission and fruit and leaf abscission are regulated by different processes, at least during this early period of fruit development (Denis, 2002).

NAA was the first chemical to be used extensively for thinning; hence more work has been done with NAA than with any other chemicals. Several mechanisms were proposed to explain the thinning action of NAA. Luckwill (1953) noting that seed abortion was common in fruitlets sprayed with NAA, proposed that this response reduced the ability of some fruits to compete for nutrients, leading to abscission. Other researchers found that NAA can thin several cultivars without affecting seed number (Batjer and Thompson, 1961). Eberth and Banghert (1982) presented data indicating that NAA reduces auxin synthesis and transport from the fruit to the abscission zone. They measured extractable and diffusible auxin content of apple fruitlets following application of carbaryl, ethephon and NAAm. They concluded that reduced auxin transport was the major factor responsible for the thinning action of all three compounds, but the inconsistencies in their data make the conclusion questionable. Auxin applications stimulate ethylene production in many plant tissues, and this increase in the concentration of ethylene could induce abscission. When Ebert and Bangerth (1982) compared the effect of three thinning agents (see above) on apple fruitlet abscission they found high ethylene evolution after ethephon treatment, while NAAm provoked a weak ethylene response, whereas carbaryl had none. They concluded that ethylene evolution of itself was not sufficient to induce abscission. The possible effect of NAA in inhibiting photosynthesis will be discussed in next chapter.

BA has been used as a thinner shorter time than NAA, and therefore its mechanism of action has not been studied extensively. Application of BA stimulated ethylene production in both leaves and fruits and the rate of evolution increased with the concentration applied (Greene *et al*., 1992). The thinning response did not follow ethylene evolution and they concluded that BA might reduce the supply of sugar to the fruit. Yuan and Greene (2000) observed stimulation of dark respiration after BA application and put a hypothesis that reduced carbohydrate supply to the fruitlets leading to its abscission.

Ethephon is an old well known compound which hydrolysed in tissue and release ethylene. After than the fruitlet abscission occurs, before and at the time of June drop or at harvest time. Thus, a logical hypothesis that fruit thinning agents (as NAA, BA, ethephon) stimulate ethylene evolution and this is the base for fruitlet abscission. But only when ethephon was used the ethylene evolution increased dramatically; other agents had little effect on ethylene evolution, carbaryl had none and thinning response did not parallel fruit ethylene content. This suggests that ethylene is not the primary factor controlling fruitlet abscission.

The mode of action of three new thinning compounds also does not give equal answer for the main reason of starting the fruitlet abscission process:

Thinning properties of abscisic acid (ABA) was proved on apples and pears and the most effective time of application is at 10 mm fruitlet diameter (Greene *et al*, 2011). ABA is a naturally occurring hormone which has the key function in the regulation of stomata movement. Closing the stomata, thus reducing photosynthesis and restricting carbohydrate supply should be the important factor contributing to fruitlet abscission.

Aminocyclopropane-1-carboxylic acid (ACC) is the new, promising but not yet registered thinning agent where reports exist on successful thinning of pome and stone fruits. ACC is the natural occurring compound presenting one of the last steps in ethylene biosynthetic pathway. Application of ACC results in rapid evolution of ethylene and this may be the mode of action of this thinner. A consistent results coming from apple thinning experiments while on plums and pear trials variable thinning is reported (Greene and Costa, 2013).

Metamitron (Brevis) is the photosynthetic inhibitor, originally herbicide functioning through inhibition of photosystem II where blocking the electron transport and chlorophyll fluorescence is enhanced. Metamitron has been reported to be quite active as a thinning agent for pome-fruits, mainly for apple and pear (McArtney and Obermiller, 2012). The phytotoxicity occurred on some leaves but the effect is only temporary and does not influence fruit finish.

Photosynthesis inhibition and fruitlet thinning

On last year’s more and more evidence is provided in support of assimilation-dependent fruitlet abscission process. Even a small reduction of photosynthate translocation to the fruitlet can cause its abscission (Schumacher *et al*., 1987). Canopy light interception reduced to 60-90% of full sunlight throughout a year can cause significant apple fruitlet abscission (Doud and Ferree, 1980). Byers *et al.* (1986, 1990, 1991) showed that reducing light interception by 90% when fruitlets were 8-33 mm in diameter caused dramatic fruitlet abscission, similar to the application of photosynthetic inhibitors. They found that after 3 day of artificial shade fruit stopped growing and dropped 7-12 days later. They suggested that thinning chemical may interfere with photosynthesis leading to a deficiency of carbohydrates. When shading is followed by chemical thinning, fruitlet abscission can be excessive (Lehman *et al*, 1987). Stopar *et al.* (1997) found that NAA application inhibited carbon assimilation by as much as 25% in ‘Delicious’ and ‘Empire’ leaves and some inhibition was evident for as long as 2 weeks. In the same experiment Stopar *et al.* (1997) did not find negative influence of BA on net photosynthesis. However, Yuan and Green (2000) reported that net photosynthesis was reduced 10-15% following application of BA at 50 or 100 mgL^{-1}. If the 4 days of 80% shade was administered immediately following thinner application (carbaryl 1000 $mg.L^{-1}$ or NAA 7 $mg.L^{-1}$), trees was nearly defruited. Administering a shading treatment for 4 days prior to thinner application had no influence on altering the thinner response to fruitlets.

Quinlan and Preston (1971) described how the competition among fruitlets and shoots for photosynthates limited the fruitlet set after June drop. Dennis (1986) reported that king fruitlets abscised less due to their major position in the cluster. Black *et al*. (2000) noted that the application of NAA or BA reduced the number of spurs bearing multiple fruits. Fruitlets in competition in the cluster, king fruitlets in competition with laterals and laterals in competition with kings and other laterals, abscised more than comparable fruitlets without competition in the cluster (Stopar, 1998). Lateral fruitlets were more subjected to abscission compared to king fruitlets and started to abscise at least 3-days earlier than king fruitlets (Kolarič *et al*., 2016).

A photosynthesis inhibitor metamitron has been recently reported to provoke fruitlet thinning effect if applied in very small amount comparing to its application as herbicide. Successful apple and pear fruitlet thinning with the use of metamitron was observed from many trials (Dorigoni and Lezzer, 2007; Clever 2007; McArtney and Obermiller, 2012) and was reported from many research station working in the frame of EUFRIN Working Group for Fruit Thinning (Costa, personal communications). Because of the suitable fruitlet thinning effect the manufacturing company was quite active in the past few years and prepared metamitron (with commercial name Brevis) for thinning agent purpose and went into registration for Europe and some other countries. Green and Costa (2013) summarized thinning properties of metamitron:

- The effect are concentration dependent,
- The application window is from 8 to 14 mm king fruit diameter for maximum response, but some thinning activity can be achieved up to 20 mm,
- The chemical was shown to be active in most of the cultivar tested so far,
- The phytotoxicity, although present, is temporary and it does not appear to adversely affect fruit finish, fruit quality, and productivity or return bloom.

Mostly two applications of metamitron are sprayed, first at 6-8 mm and secondly at 12-14 mm of king fruit diameter, and the final fruit set is mostly the sum of both applications. Internal fruit quality increased according to the reduction of crop load (Lafer, 2010). Adaptation the dosage to predicted light intensity at the time of application and/or a few days later seems crucial for thinning response of metamitron.

Conclusion

When thinning agents were applied prior to the ’June drop’ period they accelerated natural process of fruitlet abscission. Fruitlet drop are not accompanied by leaf abscission, nor do thinning agents induce leaf abscission when applied at this time. Processes of leaf abscission are much better explained than fruitlet abscission. Research is needed to provide a better understanding of the mechanism of action of chemical fruitlet thinners. The role of ethylene evolution following some chemical thinner applications is mostly considered as the final step of fruitlet abscission process, and not as the initial trigger. More support is given to the basic role of auxins and/or translocation of auxins when fruitlets in the cluster compete for setting in the so called “correlatively triggered” abscission process. Fruitlets with higher auxin transport sets better. At the same time more competition for carbohydrates in the fruitlet cluster provoked strong assimilation shortage and this may be the reason of weak fruitlet set. The connection between hormonal and/or assimilation reasons for apple fruitlet is not well explained yet. The effects of chemicals in inhibiting photosynthesis possibly in conjunction with shading experiments should be investigated more systematically to determine how important this effect is in inducing abscission.

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