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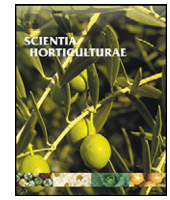

Correlative polar auxin transport to explain the thinning mode of action of benzyladenine on apple

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ABSTRACT

Chemical thinning of young apple (*Malus domestica*, Borkh.) fruit has become standard agricultural practice worldwide. The general understanding about the mode of action of thinning substances is, however, still very limited. Benzyladenine (BA), one of the most promising newer thinning chemicals has been chosen as an example to study its “mode of action”. The following aspects were investigated: (1) the site of action, (2) effects on seed number and development, (3) fruit and vegetative growth, (4) photosynthesis and (5) polar indoleacetic acid transport (IAA_{PAT}). When BA was applied at 100 mg L^{-1} on three apple cultivars on whole trees or leaves-only, thinning effects were comparable to or even stronger than hand thinning. BA applied only on fruit showed insignificant thinning. At June drop the weight of abscising fruit was comparable or even higher when treated with BA. Growth of remaining fruit was not affected until harvest when only fruit were treated. However, when leaves-only or whole trees were treated remaining fruit showed a decreased fruit growth initially but surpassed control fruit thereafter. No direct correlations were found between thinning efficacy and seed number, shoot growth, photosynthesis and by indirect conclusion, assimilate allocation. Thus, these assessments provided no clear explanation for a possible mode of action of BA. Remarkably, a decrease in IAA_{PAT} of lateral fruit was opposed to an increase in IAA_{PAT} of bourse shoot tips after BA application. This was only observed when leaves/shoot tips but not fruit only were treated. Assuming a correlative IAA transport autoinhibition (ATA) of fruit by the IAA_{PAT} of shoots, particularly of bourse shoot tips, may explain fruit abscission and the mode of action of BA applications in apple. The latter aspects are discussed in more detail.

1. Introduction

Flower or fruit thinning is one of the most effective practices in apple to improve fruit quality, return bloom and to reduce and save hand thinning and harvest costs (Bangerth, 2000, 2009; Link, 2000; Tromp, 2000). Hand thinning is often impractical because of labor costs and availability. Therefore, extensive research is devoted to find new effective and environmentally acceptable chemical thinners (Dennis, 2000). Abscission of young fruit is a complex process and under the control of numerous tree factors like vegetative growth, tree age, flower quality, cultivar and rootstock, besides environmental effects like temperature, light intensity and quality (Dennis, 2000; Byers et al., 1990; Williams, 1979). Chemical thinning is considered as an enhancement of the natural abscission process but the mechanisms by which these factors affect thinning are still largely unknown (Schröder and Bangerth, 2006) as well as the effects of weather conditions before, during or after application (Black et al., 1995). This makes applications of thinning substances and investigations on their mode of action rather difficult (Dennis, 2000; Schönherr et al., 2000).

Abscission of plant organs requires the activation of an abscission layer (Addicott, 1982), by ethylene (Osborne, 1989) and its inhibition by a polar basipetal indoleacetic acid (IAA_{PAT}) transport from the distal fruit or leaf through the abscission zone layer (AZ) (Addicott, 1982). Synthesis and action of these two hormones have therefore, been intensively investigated in relation to natural and chemically induced fruit drop with focus on carbaryl, ethephon and naphthylacetic acid (NAA) (Drazeta et al., 2004; Sexton, 1994; Ebert and Bangerth, 1982).

The naturally occurring cytokinin benzyladenine (BA) used in our experiments and described herein, is one of the newer apple thinning compounds with proven thinning efficacy in apple (Basak, 2006; Costa et al., 2004; Greene, 1993; McArtney et al., 1995). Besides its thinning effect, BA can stimulate and control a wide range of physiological and developmental processes in plants (Davis, 1995). Accordingly, BA has been found by many researchers to increase fruit size, fruit firmness and return bloom independently of its thinning effect (Bangerth, 2009; Basak, 1996;

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Wismer et al., 1995; Elfving and Cline, 1993; Greene, 1993; Bound et al., 1991). BA thins over a wide range of concentrations of 25–200 mg L^{-1} depending on cv. (Basak, 1996; Bound et al., 1993, 1991; Greene and Autio, 1989) and thins from bloom to 3 weeks after full bloom with a maximum thinning response when applied at a king fruit (KF) diameter of 8–12 mm, which is approximately 10–25 d after full bloom (Basak, 1996; McArtney et al., 1995; Bound et al., 1993, 1991; Greene and Autio, 1990, 1989). BA efficacy may be negatively affected by maximum daily temperatures below 15–18 °C (Bound et al., 1997).

BA's mode of action has not been studied extensively and is not well understood (Dennis, 2000). BA was more effective as a thinner when applied to leaves/shoots alone than to fruit-only (Greene et al., 1992). However, fruit size was increased when BA was applied only to fruit and this size increase occurred even in the absence of a significant thinning effect (Dennis, 2000). BA showed no negative effects on leaf photosynthesis. Stopar et al. (2000, 1997), Wang and Rom (1987) and Mauk et al. (1986) as well as Yuan and Greene (2000a) reported an increase in sink-activity of fruit treated with BA. Application of BA stimulated ethylene production in both leaves and fruit, but ethylene could not explain the mode of action of BA (Dal Cin et al., 2007; Dennis, 2000; Stopar et al., 2000; Greene et al., 1992). BA applications can significantly reduce seed numbers (McArtney et al., 1995; Elfving, 1989) even if only fruit were treated and no thinning occurred (Greene et al., 1992). Recently Yuan and Greene (2000a,b) concluded that BA may thin fruit by increasing dark respiration and decreasing net photosynthesis. Overall, the mode of action of BA as a chemical thinner remains unclear (Dal Cin et al., 2007).

As a naturally occurring plant hormone BA's exclusive action via leaves/shoot tips and not fruit caught our special attention in trying to understand correlative regulatory mechanisms between leaves/shoots and fruit. We investigated the IAA_{PAT} of the bourse shoot and its interaction with the IAA_{PAT} of fruit together with the most important parameters previously discussed in the literature. Thus, to develop a hypothesis on the mode of action of BA it was necessary to discuss significant and non significant results in order to rule out those which are most certainly not involved.

2. Materials and methods

2.1. Plant material and location

All experiments were conducted at the Horticultural Research Center for fruit production at Lake Constance, Bavendorf, Germany. Three experiments were performed over two consecutive seasons on the cultivars 'Golden Delicious' (season 1), 'Elstar' and 'Jonagold' (season 2). Six to eight years old Super Spindle trees on Malling 9 (M.9) rootstock at a density of 9090 (2.75 × 0.40 m) trees/ha were carefully selected for uniformity in tree size and flower intensity. For each treatment nine single tree replicates were arranged in completely randomized blocks. Four trees were used for destructive leaf and fruit sampling/analyses and the remaining five trees were assessed for thinning efficacy and non-destructive determinations.

2.2. Treatments

The following eight treatments were conducted: untreated control (UTC); hand thinning (HT) by cutting all flowers from two of every three clusters per tree at full bloom; BA (1.9% w/w, Abbott Laboratories, Abbott Park, IL) applied at 50 or 100 mg L^{-1} active ingredient on whole trees; BA at 100 mg L^{-1} on fruit-only or leaves-only (entire tree); Shoot tip squeezing (STS) with or without BA at 100 mg L^{-1} on whole trees. All BA applications were conducted at 14–18 d after full bloom (DAFB) when KF diameters were 10–12 mm and maximum daily temperatures reached 18–25 °C at application and in the following days. The relative humidity ranged from 42% to 47% and conditions were clear and dry. All spray solutions contained 0.1% Tween 20 (Serva, Heidelberg, Germany) and were applied to run-off. For whole-tree sprays a knapsack sprayer was used. When only leaves were treated, all fruit clusters/tree were individually covered with plastic bags before treatment and removed when dry. When only fruit were treated, nearby leaves were spray-protected by a removable rubber plate. Leaves and fruit alone were treated with a hand held sprayer. Preliminary experiments showed that both methods to protect either leaves or fruit during spraying did not affect fruit set (data not presented). Where STS was conducted all shoots/tree were squeezed from 2 d after BA application and repeated at weekly intervals when re-growth occurred and until vegetative growth ceased shortly before June drop. STS was conducted lightly to inhibit terminal shoot growth but to avoid inducing lateral bud break.

2.3. Determination of fruit set, thinning selectivity and fruit weight

All flower clusters/tree were counted at full bloom. Fruit number/tree were recorded after flower drop (initial set), June drop and at-harvest (final set). Fruit set as fruit/100 flower clusters was calculated for each assessment date. After June drop, 90 fruiting sites (45 on each side of a tree) were randomly selected for five trees. Fruit/site were counted and fruit were classified as KF and LF to determine thinning selectivity. For fruit weight determination, 24 firmly attached LF/tree or abscising fruit when touched were randomly sampled and weighed at four assessment dates from 3 to 22 d after treatment (DAT).

2.4. Determination of seed and vegetative growth effects

In 'Golden Delicious' and 'Jonagold', 45 firmly- and 45 loosely attached LF from each treatment were randomly sampled at June drop and stored at −20 °C. Later in the season the number of fully developed and under-developed seeds/fruit was visually determined and 100 seeds were dried at 60 °C and weighed. In 'Elstar' and 'Golden Delicious', the number and length of all shoots of five trees were measured at 1, 14 and 142 DAT (at harvest). At harvest the number and length of all bourse shoots/tree were separately assessed. For each tree all shoot values were related to the trunk cross sectional area (TCSA) as measured at-harvest. In 'Elstar' and 'Golden Delicious', the area of 50 leaves randomly sampled per tree was measured when June drop peaked using a leaf area meter (AM 100; ADC BioScientific Ltd., Hoddesdon, England). Additionally, in 'Elstar' all leaves/tree were counted at 34 DAT and the total leaf area/tree, TCSA and fruit was calculated.

2.5. Fluorescence- and photosynthesis determinations

Fluorescence measurements (CF) were conducted on all three cultivars. Thirty leaves were randomly taken from each treatment at 1, 2 or 7 DAT. For fluorescence measurements a fluorometer (PAM 2000; Walz, Effeltrich, Germany) was used following the method as described by Schreiber et al. (1986).

In 'Elstar' and 'Golden Delicious', CO_2-assimilation rate, transpiration rate, stomatal CO_2-conductivity and internal CO_2-concentration of spur leaves (second oldest leaf) or bourse shoot leaves (third or fourth leaf from the shoot base) were measured in the orchard with an infrared gas analyzer (Ciras PN Auto; PP Systems, Hitchin, UK). Measurements were taken on a minimum of six leaves of five trees/treatment 2 and 6 DAT between 10.00 and 12.00 hrs at saturating light conditions (1000–1400 μmol m^{-2} s^{-1})