Non-structural carbohydrate status and CO₂ exchange rate of apple fruitlets at the time of abscission influenced by shade, NAA or BA

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Abstract

Four days of 90% shading at the time of fruit setting (1–5 days after petal fall, DAPF) of mature ‘Jonagold’/M.9 apple trees was combined with the application of thinning agents to establish the possible interaction of both main treatments on fruit retention, and the effects of the main treatments on fruitlets CO₂ exchange and their carbohydrate concentration. Shading alone reduced yield by up to 35%. When shading was followed by the application of 15 ppm 1-naphthaleneacetic acid (NAA) or 50 ppm 6-benzyladenine (BA), the interaction between shading and chemical thinners was on the border of significance. Following the assumption that abscission was induced by shading before the application of chemical thinning agents, the same process of diminished dark respiration rate ($R_d$) was found on fruitlets sampled 3 days after the end of shading and 7 days after NAA and BA spraying, i.e. in the fruitlets that were considered prone to drop. A week after the end of shading the abscission of fruitlets due to shading was completed and on the remaining fruitlets that were not prone to abscission any more, larger negative net CO₂ assimilation rates ($A$) and enhanced $R_d$ were recorded. Fruitlets prone to abscission sampled 2 days after the end of shading showed a lower concentration of glucose and ascorbic acid and a higher concentration of starch. Eight days after the end of shading, the fruitlets from shaded trees that were not prone to abscission any more contained less fructose while the fruitlets from NAA and BA sprayed trees had a higher concentration of fructose a week after application. The results do not support the hypothesis that a good assimilate supply is needed for the retention of apple fruitlets, because the fruitlets retained on trees expressed even stronger CO₂ loss and because the concentration of non-structural carbohydrates did not decrease in fruitlets prone to drop with the exception of glucose.

Keywords: Apple; Fruit set; Shading; NAA; BA; Carbohydrates; Ascorbic acid; Fruitlets CO₂ exchange

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1. Introduction

Apple trees normally set too many fruitlets, so chemical thinning is a standard practice in the orchard. The mechanism of apple fruitlet abscission is still not completely understood. It depends on many factors and their interactions, so it cannot be predicted satisfactorily (Wertheim, 1998). Natural fruitlet abscission is excessive in some years and minimal in others (Greene, 1989).

Reduced canopy light interception during certain periods shortly after flowering causes a significant apple fruitlet abscission (Jackson and Palmer, 1977; Doud and Ferree, 1980). Five days of 90% shading in the period when apple fruit diameter grew from 8 to 33 mm induced dramatic fruitlet abscission similar to that caused by the application of photosynthetic inhibitors (Byers et al., 1986, 1990a). Excessive fruit drop occurred when heavy shading followed the application of a chemical thinner (Lehman et al., 1987).

It is not clear whether the retention of fruitlets in the cluster depends on the inflow of photosynthates or the abscission of fruitlets depends on the momentary hormone situation in a plant (Sexton et al., 1989; Arteca, 1995). Various growth regulators used for apple thinning interfere with endogenous hormones (Bangerth, 1986). Brenner et al. (1989) suggest that endogenous hormones are the main factors governing photosynthate translocation to the fruitlets. Assimilation partitioning is subject to hormonal regulation (Daie, 1989).

Suppressed transport of metabolites from foliage to fruitlets following naphthaleneacetic acid (NAA) spraying is the primary mechanism that stimulates abscission of the first drop of apple fruitlets (Schneider, 1978; Mauk et al., 1986). Spraying with 15 ppm NAA as a chemical thinner consistently suppressed the CO₂ assimilation rate of leaves. Such an effect was not observed after a 50 ppm benzyladenine (BA) application (Stopar et al., 1997). The content of non-structural carbohydrates in fruitlets was lowered after 10 days of 92% shading or after the application of 100 ppm of the photosynthesis inhibitor terbacil (Polomski et al., 1988). On the contrary, Berüter (1985) demonstrated that fruitlet abscission during the early summer period was not related to the carbohydrate concentration of the fruit. A highly reduced but still negative net CO₂ assimilation rate of fruitlets was the indicator of abscission after shading and terbacil application (Stopar, 1998).

Goldwin (1989) found that only a limited amount of metabolites from neighboring foliage or from reserves was translocated to the apple flower at the time of fruit setting. Flowers contributed significantly to the chlorophyll content of the flower cluster at the green cluster stage, so that the flower photosynthesis contributed 15–33% to their carbohydrate balance during the flowering and fruit setting periods (Vemmoss and Goldwin, 1993, 1994).

As several researchers speak in favor of the importance of photosynthates supply for apple fruitlet retention, we tried to verify the carbohydrate theory for...
fruitlet abscission. The experiment was conducted to measure apple fruitlet CO$_2$
assimilation and their carbohydrate status on fruitlets prone or not prone to drop
because of a few days of artificial shade or application of apple thinning agents,
NAA and BA. The objective of this research was to: (1) study the net CO$_2$
assimilation rate ($A$) and the dark respiration rate ($R_d$) of apple fruitlets before
abscission was induced by shade, NAA or BA; (2) determine the concentration of
individual non-structural carbohydrates in fruitlets prone to abscission; and (3)
evaluate fruit retention after any possible interaction between 4-day shade
equivalent to very cloudy weather) and two frequently used thinning agents,
NAA and BA.

2. Materials and methods

We chose 7-year-old apple trees ‘Jonagold’/M.9 homogenous as to blooming
and vigor, growing in the experimental orchard at Brdo in continental Slovenia.
The experimental design was a factorial in randomized blocks with six re-
A
plications. Each treatment was applied to a whole single-tree plot. The factorial
3×2 (chemical agents×light) experiments were conducted in the years 1997 and
1998 with the following six treatments:

1. control, non-shaded;
2. control, shaded;
3. NAA (15 ppm) application=0.45 ml RP1 l$^{-1}$ (Pinus, Rače, Slovenia), non-
shaded;
4. NAA (15 ppm) application=0.45 ml RP1 l$^{-1}$ (Pinus, Rače, Slovenia), shaded;
5. BA (50 ppm) application=2.8 ml Accel l$^{-1}$ (Abbott Laboratories, Long
Grove, Ill.), non-shaded;
6. BA (50 ppm) application=2.8 ml Accel l$^{-1}$ (Abbott Laboratories, Long
Grove, Ill.), shaded.

Shading was accomplished by making tents around trees using a dark
agrotexile covering, Covertan® (non-woven polypropylene, Corovin, Hannover,
Germany). Covertan® reduced the photosynthetic photon flux density (PPFD) to
10\% of that measured outside the tent, so the PPFD under Covertan® on sunny
days was 80–100 μmol m$^{-2}$ s$^{-1}$. These levels are equivalent to the PPFD under
very cloudy conditions (Hočevar et al., 1982). The PPFD inside and outside the
tent was measured with a Sunfleck Ceptometer (Decagon, Washington, USA).
The agrotexile tents were open 30 cm above ground to allow aeration and
prevent canopy overheating. In 1997, 4 days shading was set at 6 mm king fruit
diameter (KFD), i.e. 1 day after petal fall (DAPF), and in 1998, at 9 mm KFD (5
DAPF). In both years the weather was mostly sunny during the 4 days of shading.
Application of chemical agents was done with a hand sprayer until run-off just
after uncovering the trees, i.e. in 1997 at 10 mm KFD and in 1998 at 13.5 mm
KFD. KFD as a measure of phenological stage was obtained as the average diameter of 30 fruitlets on untreated trees.

In 1997, we set two identical experiments in neighboring regions. The first one was conducted to estimate the effect of treatments on yield and the second experiment was used for sampling the fruitlets for non-structural carbohydrates, ascorbic acid and CO₂ exchange measurements. In 1998, we designed the same experiment for repeating fruitlet assimilation measurements. In order to study assimilation, non-structural carbohydrates and the ascorbic acid status of fruitlets before the beginning of the abscission process, we sampled the fruitlets which did not show yellowing or any sign of abscission at the time of picking. To distinguish fruitlets on the tree that are prone to abscission versus the fruitlets that are not, we observed fruitlets drop and measured the weight of the sampled fruitlets. According to measurements made by Stopar (1998), a 90% PPFD reduction and 7–12 DAPF caused the drop of fruitlets for up to 8 days later, while no thinning was observed on these trees later. At the end of 90% shading or 8 days after terbacil application, the fruitlet size was smaller and these fruitlets were more prone to abscission. Similarly, Byers et al. (1991) reported that after 3 days of artificial shade, fruitlets stopped growing from the last day of shading up to 6 days after shading and dropped 6–12 days later.

Gas exchange measurements of sampled apple fruitlets were done in 1997, 2 and 8 days after chemical application, and in 1998, 3 and 7 days after chemical application. A and Rₐ of fruitlets were measured with a portable ADC LCA 3 infra-red CO₂ analyzer (ADC, Hoddesdon, UK) equipped with a Parkinson coniferous chamber. To obtain a good average per tree, six lateral fruits and two king fruits, each from different clusters, were cut and placed in the chamber. The open system of CO₂ exchange measurement provided a net flow of air through the chamber and the CO₂ assimilation of the fruitlets was determined by comparison of the CO₂ concentration at the inlet and the outlet of the chamber. The air was dried prior to entering the chamber to 10% RH and after the setting of steady-state conditions the outlet air was leaving the chamber with approximately 50% RH. The temperature in the chamber was 2–6°C higher than outside but did not exceed 30°C. After approximately 1 min, at steady-state CO₂ exchange, A was recorded in the condition of saturated light (>1000 μmol m⁻² s⁻¹ PPFD). Rₐ was measured by placing the chamber with the same fruitlets in a dark box for about 1 min. At the end of the photosynthesis measurements the fruitlets were weighed to express the gas exchange per gram of fresh mass. In the preliminary fruitlet CO₂ exchange measurements, we did not observe any difference between the attached and severed fruitlets. According to Jones (1981), CO₂ exchange measurements of detached apple fruit were consistent with those made on attached fruit in the field.

Fruitlet samples used for determination of the concentration of non-structural carbohydrates and ascorbic acid were picked just after the assimilation
measurement was done in 1997. Samples contained about 100 fruitlets per tree. Sucrose, glucose, fructose and sorbitol were determined by HPLC (Hewlett-Packard 1100) according to Vemmos (1995). The starch in fruitlets was analyzed according to the enzyme method proposed by Boehringer Mannheim (Germany). Ascorbic acid was determined spectrophotometrically (Roe, 1951).

Data were subjected to factorial analysis of variance using a statistical software program, Statgraphics 5.0 (STSC, Rockville, USA).

3. Results

3.1. Effect on fruitlet CO₂ exchange

A significant effect of shading on fruit retention data was recorded at harvest in 1997. Four days of 90% shading (1–5 DAPF) diminished the yield by 35%. The number of fruit at harvest was also reduced by 35% when the shaded non-chemically thinned treatments were compared with the control (Table 1). Application of chemical thinning agents NAA (15 ppm) and BA (50 ppm) significantly affected the fruit retained at harvest. NAA spraying after the end of shading slightly enhanced fruitlets abscission while no additional thinning occurred when shading was followed by BA application. The effect of interaction between shading and chemical thinners on fruit retention at harvest was on the border of significance.

Light reduction and the subsequent application of 15 ppm NAA or 50 ppm BA showed no effect on fruit A or \( R_d \) 2 days after chemical spraying, but the average weight of fruitlets from shaded trees (used for assimilation measuring) was significantly lower (Table 1). According to Byers et al. (1991) and Stopar (1998) it can be assumed that the lower weight of fruitlets from shaded trees was the consequence of shading and that the fruitlets had already fallen in the process of abscission.

Eight days after chemical application (13 DAPF), no differences were observed in fruitlet weight any more (Table 1). All sampled fruitlets in our measurement carried out 8 days after chemical application did not show a tendency to abscission and looked healthy, because the larger part of fruit drop from shaded trees was already completed. Stronger abscission of fruitlets from shaded trees was evident on the ground. So the CO₂ exchange data 13 DAPF of fruitlets from shaded trees should be understood as data of fruitlets which were not inclined to abscission any more. Significantly more negative A and stronger \( R_d \) was recorded on fruit from shaded trees 13 DAPF (Table 1). CO₂ loss in fruitlets from shaded trees was significantly enhanced compared to fruit A from non-shaded trees. Thinning agents did not show any effect on fruitlets A or \( R_d \) in the year 1997.
Table 1
Net CO₂ assimilation rate ($A$), dark CO₂ respiration rate ($R_d$) and apple fruitlet weight of ‘Jonagold’/M.9, 2 and 8 days after chemical applications (7 and 13 DAPF, respectively). The fruit retained at harvest in factorial experiment $3 \times 2$, 1997

<table>
<thead>
<tr>
<th>Treatment</th>
<th>2 Days</th>
<th>8 Days</th>
<th>Yield TCSA (kg cm⁻²)</th>
<th>No. of fruits per cm² TCSA</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>$A \times 10^{-4}$ (µmol g⁻¹ s⁻¹)</td>
<td>$R_d \times 10^{-4}$ (µmol g⁻¹ s⁻¹)</td>
<td>Fruitlet weight (g)</td>
<td>$A \times 10^{-4}$ (µmol g⁻¹ s⁻¹)</td>
</tr>
<tr>
<td>Control, non-shaded</td>
<td>−28.0</td>
<td>64.0</td>
<td>0.65</td>
<td>−6.3</td>
</tr>
<tr>
<td>Control, shaded</td>
<td>−27.2</td>
<td>63.2</td>
<td>0.47</td>
<td>−23.6</td>
</tr>
<tr>
<td>NAAc, non-shaded</td>
<td>−27.6</td>
<td>66.0</td>
<td>0.65</td>
<td>−6.7</td>
</tr>
<tr>
<td>NAA, shaded</td>
<td>−31.2</td>
<td>69.8</td>
<td>0.47</td>
<td>−25.1</td>
</tr>
<tr>
<td>Ba₄, non-shaded</td>
<td>−32.0</td>
<td>67.7</td>
<td>0.60</td>
<td>−5.6</td>
</tr>
<tr>
<td>BA, shaded</td>
<td>−28.7</td>
<td>60.5</td>
<td>0.53</td>
<td>−22.3</td>
</tr>
</tbody>
</table>

$F$ significance

- Thinning agents (A): NS
- Shading (B): NS
- Interaction (A×B): NS

**NS** represents non-significant, ***,* ** significant at $P \leq 0.05$, and $P \leq 0.001$, respectively.

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a DAPF: days after petal fall; TCSA: trunk cross-sectional area.
b Shading on 90% PPFD reduction for 4 days (1–5 DAPF).
c NAA 15 ppm application 5 DAPF, at 10 mm mean KFD.
d BA 50 ppm application 5 DAPF, at 10 mm mean KFD.
e NS represents non-significant, ***,*, * significant at $P \leq 0.05$, and $P \leq 0.001$, respectively.
Gas exchange measurements carried out in 1998, 3 days after the end of a 4-day shading (11 DAPF), showed a significantly depressed $R_d$ of fruitlets from shaded trees compared to non-shaded treatments (Table 2). The average fruitlet weight based on CO$_2$ measurements was significantly lower for “shaded” fruit, so the diminished $R_d$ could be explained as a sign of fruitlets prepared for abscission. Three days after NAA (15 ppm) and BA (50 ppm) application, no significant effect of chemical thinners on fruit gas exchange measurement was observed.

Fruitlet weight 7 days after the end of shading (15 DAPF in 1998) did not show any difference between shaded and non-shaded treatments (Table 2). Most of the fruits from shaded trees had already abscised as in the year before. The $R_d$ of the remaining fruitlets on shaded trees, which did not tend to abscise any more, was significantly higher and consequently, $A$ was more negative (greater CO$_2$ loss). Photosynthesis measurements 7 days after chemical applications showed a significant effect of chemical thinners on $A$ and $R_d$. Reduced $R_d$ and less negative $A$ were recorded on NAA and BA thinned fruitlets.

### 3.2. Effect on fruitlet carbohydrate and ascorbic acid concentration

Measurement of fruitlet carbohydrates 2 days after the end of a 4-day 90% PPFD reduction (7 DAPF, 1997) showed a significantly lower concentration of glucose and a higher concentration of starch in the fruit from shaded trees (Table 3). The ascorbic acid concentration in the same fruitlets (prone to abscission because of shading) was lower.

Eight days after the end of shading (13 DAPF, 1997) a significant effect of shading and chemical thinners on fructose concentration was found (Table 4). Because of a 4-day shading the first drop of fruitlets was already completed 13 DAPF, so that the reduced amount of fructose was the sign of healthy fruitlets not prone to dropping. In accordance with this, the fructose concentration was enhanced in the fruitlets 8 days after NAA and BA application, i.e. in the fruitlets that were prone to abscission because of the action caused by thinning agents. The sucrose concentration fell below the level of detection 13 DAPF.

### 4. Discussion

The influence of shade on apple fruit abscission at the sensitive period 1–4 weeks after petal fall, was reported by Polomski et al. (1988) and Byers et al. (1991). Lehman et al. (1987) and Byers et al. (1990b) observed an additional thinning when heavy shading in early summer was combined with chemical thinning. In our experiment, 4 days of 90% PPFD reduction (1–5 DAPF) significantly reduced the yield on mature apple trees ‘Jonagold’/M.9. Application of a thinning agent NAA (15 ppm) to shaded trees caused a slightly stronger fruit
Table 2
Net CO₂ assimilation rate (A), dark CO₂ respiration rate (Rₜ) and apple fruitlet weight of ‘Jonagold’/M.9, 3 and 7 days after chemical applications (11 and 15 DAPF, respectively) in factorial experiment 3×2, 1998

<table>
<thead>
<tr>
<th>Treatment</th>
<th>3 Days</th>
<th></th>
<th>7 Days</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>A×10⁻⁴</td>
<td>Rₜ×10⁻⁴</td>
<td>Fruitlet weight (g)</td>
<td>A×10⁻⁴</td>
</tr>
<tr>
<td>Control, non-shaded</td>
<td>−19.1</td>
<td>34.4</td>
<td>1.47</td>
<td>−10.7</td>
</tr>
<tr>
<td>Control, shaded</td>
<td>−10.8</td>
<td>22.4</td>
<td>0.85</td>
<td>−31.7</td>
</tr>
<tr>
<td>NAA⁵, non-shaded</td>
<td>−19.1</td>
<td>35.6</td>
<td>1.40</td>
<td>−6.7</td>
</tr>
<tr>
<td>NAA, shaded</td>
<td>−20.3</td>
<td>31.5</td>
<td>0.86</td>
<td>−9.8</td>
</tr>
<tr>
<td>Ba⁶, non-shaded</td>
<td>−18.1</td>
<td>34.7</td>
<td>1.25</td>
<td>−7.8</td>
</tr>
<tr>
<td>BA, shaded</td>
<td>−16.1</td>
<td>29.9</td>
<td>0.89</td>
<td>−18.2</td>
</tr>
</tbody>
</table>

F significance⁷

<table>
<thead>
<tr>
<th></th>
<th>3 Days</th>
<th></th>
<th>7 Days</th>
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<tr>
<td></td>
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</tr>
</tbody>
</table>

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⁷ NS represents non-significant, *, **, *** significant at P≤0.05, P≤0.01, and P≤0.001, respectively.

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⁵ NAA 15 ppm application 8 DAPF, at 14 mm mean KFD.

⁶ BA 50 ppm application 8 DAPF, at 14 mm mean KFD.

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⁷ Shading on 90% PPFD reduction for 4 days (5–8 DAPF).
drop noted at harvest compared to NAA application on non-shaded trees. In contrast, no additional thinning occurred when shading was followed by BA (50 ppm) application. The interaction between thinning agents and shading for fruit retention at harvest was on the border of significance.

Vemmos and Goldwin (1994) estimated that flower photosynthesis significantly contributed to its carbohydrate balance during the fruit setting period. The fruit photosynthesis in our experiments did not exceed the respiration on any occasion.

Table 3
Non-structural carbohydrate and ascorbic acid concentration in dry matter of fruitlets ‘Jonagold’/M.9 harvested 2 days after chemical applications (7 DAPF) in factorial experiment 3×2, 1997

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Starch (mg g⁻¹)</th>
<th>Glucose (mg g⁻¹)</th>
<th>Fructose (mg g⁻¹)</th>
<th>Sucrose (mg g⁻¹)</th>
<th>Sorbitol (mg g⁻¹)</th>
<th>Ascorbic acid (mg g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control, non-shaded</td>
<td>0.15</td>
<td>36.4</td>
<td>30.3</td>
<td>0.90</td>
<td>38.1</td>
<td>1.93</td>
</tr>
<tr>
<td>Control, shaded</td>
<td>0.33</td>
<td>33.2</td>
<td>29.2</td>
<td>0.85</td>
<td>40.2</td>
<td>1.53</td>
</tr>
<tr>
<td>NAA, non-shaded</td>
<td>0.20</td>
<td>35.3</td>
<td>32.0</td>
<td>0.98</td>
<td>53.8</td>
<td>2.00</td>
</tr>
<tr>
<td>NAA, shaded</td>
<td>0.37</td>
<td>32.9</td>
<td>31.1</td>
<td>1.07</td>
<td>48.1</td>
<td>1.75</td>
</tr>
<tr>
<td>BA, non-shaded</td>
<td>0.29</td>
<td>36.3</td>
<td>28.3</td>
<td>1.88</td>
<td>42.2</td>
<td>1.89</td>
</tr>
<tr>
<td>BA, shaded</td>
<td>0.40</td>
<td>31.0</td>
<td>28.6</td>
<td>1.11</td>
<td>42.7</td>
<td>1.72</td>
</tr>
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</table>

*NS significance*  

<table>
<thead>
<tr>
<th></th>
<th>Thinning agents (A)</th>
<th>Shading (B)</th>
<th>Interaction (A×B)</th>
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<tr>
<td>Thinning agents (A)</td>
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<td>**</td>
<td>NS</td>
</tr>
<tr>
<td>Shading (B)</td>
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<td>NS</td>
</tr>
<tr>
<td>Interaction (A×B)</td>
<td>NS</td>
<td>NS</td>
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</tr>
</tbody>
</table>

α NS represents non-significant, * and ** significant at P≤0.05 and P≤0.01, respectively.

Table 4
Non-structural carbohydrate and ascorbic acid concentration in dry matter of fruitlets ‘Jonagold’/M.9 harvested 8 days after chemical applications (13 DAPF) in factorial experiment 3×2, 1997

<table>
<thead>
<tr>
<th>Treatment</th>
<th>Starch (mg g⁻¹)</th>
<th>Glucose (mg g⁻¹)</th>
<th>Fructose (mg g⁻¹)</th>
<th>Sucrose (mg g⁻¹)</th>
<th>Sorbitol (mg g⁻¹)</th>
<th>Ascorbic acid (mg g⁻¹)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control, non-shaded</td>
<td>0.11</td>
<td>59.8</td>
<td>49.0</td>
<td>–a</td>
<td>36.8</td>
<td>2.04</td>
</tr>
<tr>
<td>Control, shaded</td>
<td>0.11</td>
<td>52.2</td>
<td>47.7</td>
<td>–</td>
<td>39.9</td>
<td>2.28</td>
</tr>
<tr>
<td>NAA: non-shaded</td>
<td>0.11</td>
<td>57.1</td>
<td>49.8</td>
<td>–</td>
<td>41.7</td>
<td>2.40</td>
</tr>
<tr>
<td>NAA, shaded</td>
<td>0.14</td>
<td>51.0</td>
<td>44.2</td>
<td>–</td>
<td>38.2</td>
<td>2.31</td>
</tr>
<tr>
<td>BA, non-shaded</td>
<td>0.09</td>
<td>66.3</td>
<td>50.7</td>
<td>–</td>
<td>38.2</td>
<td>2.12</td>
</tr>
<tr>
<td>BA, shaded</td>
<td>0.08</td>
<td>65.2</td>
<td>50.3</td>
<td>–</td>
<td>38.5</td>
<td>2.19</td>
</tr>
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</table>

* F significance  

<table>
<thead>
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<th></th>
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<th>Shading (B)</th>
<th>Interaction (A×B)</th>
</tr>
</thead>
<tbody>
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<td>Thinning agents (A)</td>
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<td>NS</td>
<td>NS</td>
</tr>
<tr>
<td>Shading (B)</td>
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</tr>
<tr>
<td>Interaction (A×B)</td>
<td>NS</td>
<td>NS</td>
<td>NS</td>
</tr>
</tbody>
</table>

α Below the level of detection.  

β NS represents non-significant and * significant at P≤0.05.
so that $A$ was negative which was similar to the report of Jones (1981). Two or 3 days (i.e. 1997 and 1998, respectively) after the end of shading, the fruitlets from shaded trees were smaller which should be considered as a sign of a forthcoming abscission. Stopar (1998) and Byers et al. (1991) found that after 3–5 days of artificial shade the fruitlets stopped growing at the end of shading or a few days later and that they were more prone to abscission. CO$_2$ exchange rate measurement of fruitlets 3 days after the end of shading showed a depressed $R_d$. A comparable response was found on fruitlets 7 days after NAA and BA application. On these fruitlets $R_d$ was reduced and consequently, $A$ was less negative. Assuming that chemical thinners influence fruit drop to occur later than shading, a smaller $R_d$ may be explained as a diminished metabolism of fruit starting with the abscission process (Stopar, 1998).

Byers et al. (1991) and Stopar (1998) observed a strong drop of apple fruitlets approximately 1 week after the end of 3–5 days 90% PPFD reduction. Taking into consideration that fruitlets on shaded trees 8 or 7 days (i.e. in 1997 and 1998, respectively) after the end of shading were mostly abscised, they were not taken for CO$_2$ exchange measurements. From this point of view the observed enhanced $R_d$ and more negative $A$ of shaded fruit a week after shading should be considered as a property of healthy fruits, which are not prone to abscission any more. Very strong CO$_2$ loss (probably as a consequence of strong $R_d$) of fruitlets not prone to drop does not support the hypothesis that fruitlets require a good assimilate supply for their retention. These data go together with the prediction of Byers et al. (1990b) that fruit assimilation may not be important for fruit retention.

Two days after the 4-day 90% PPFD reduction was completed a decreased glucose concentration and increased starch concentration were found in shaded fruitlets. Eight days after the end of shading, when those fruitlets prone to abscission were already abscised, a diminished fructose concentration was found in the fruitlets that were not expected to abscise any more. In contrast, the concentration of fructose was slightly enhanced in the fruitlets sampled 8 days after NAA (15 ppm) and BA (50 ppm) spraying, i.e. in the fruitlets that are probably more prone to abscission due to the action of the thinning agents.

Vemmos (1995) found an increasing level of sucrose in the fruitlets until petal fall, after which the sucrose content was dramatically decreased until 12 DAPF. No detectable level of sucrose was recorded in our fruitlets 13 DAPF.

Sorbitol is the major photosynthetically derived carbohydrate intended for translocation and conversion to other carbohydrates in apple trees (Chong and Taper, 1970; Young, 1989). No significant effect of shading or chemical thinners was found on the sorbitol concentration of fruitlets. However, data on the measurements of carbohydrate concentrations in fruitlets give some support to the theory that carbohydrate starvation of fruitlets influences their abscission. In our experiment, the fruitlets that were considered prone to drop contained more
starch, less glucose and slightly more fructose, while other non-structural carbohydrates were not influenced significantly by the applied treatments.

Ascorbic acid is a substance which could minimize oxidative stress in the plant cell and work as an antioxidant (Mckersie and Leshem, 1994). The ascorbic acid concentration in the fruitlets 2 days after the end of shading decreased in fruitlets from shaded trees. A lower concentration of ascorbic acid could be the consequence of exhausted metabolism. Shaded fruitlets, therefore, had less defence against oxidative reactions triggered by stress. A 4-day 90% shading probably caused stress which provoked the abscission of fruitlets.

References


