

Studies on the Mechanism of Fruit Abscission in Apple and Peach¹

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Abstract. Translocation of ¹⁴C-sucrose from leaf to fruit was measured in 'Golden Delicious' and 'Staymared' apple (*Malus domestica* Borkh.) and 'Redhaven' peach (*Prunus persica* (L.) Batsch) following the application of compounds reported to influence fruitlet abscission. Succinic acid-2,2-dimethylhydrazide (daminozide) reduced ¹⁴C translocation in both apple cultivars but reduced fruit set only in 'Golden Delicious'. Ethephon reduced ¹⁴C translocation and fruit set of peach. Abscisic acid (ABA) and 2,4-dinitrophenol (DNP) reduced ¹⁴C-sucrose translocation in apple. Enclosing apple limbs in black cloth bags reduced fruit set and naphthaleneacetic acid (NAA) increased leaf water potential. One method of preliminary screening of compounds for apple fruit thinning may be based on their effect on ¹⁴C-sucrose translocation from foliage to fruit.

A screening test for evaluating a compound's potential for chemical thinning tree fruits is needed (9). Martin and Brooks (13) proposed a screening technique for use with peach based on a compound's effect on ethylene evolution from leaves. However, we found little relation between the thinning effect of NAA and ethylene evolution from apple fruitlets, leaves or pedicels (22), suggesting that ethylene was not the "trigger" that initiated abscission. Furthermore, McDonnell et al. (14) reported that Alar tended to reduce apple fruit set when applied after bloom even though it apparently reduced ethylene evolution (9).

NAA reduced ¹⁴C-sucrose movement from leaf to fruit before an increase in ethylene evolution was observed (21, 22). The significance of this reduced translocation is emphasized by Hansen's report (7) that growth of young apple fruits appears to be largely dependent on current photosynthates. Lack of metabolites reaching young fruit may therefore be the causal reason for the thinning effect of NAA (21).

This report gives information on (a) the effects of several compounds on ¹⁴C-sucrose translocation, (b) the effect of shade on fruit abscission, and (c) the effect of NAA on leaf water potential. Their relation to fruit thinning is discussed.

Materials and Methods

Mature apple trees of uniform vigor and crop, growing on Malling (M) 7 stocks, and 15-year-old 'Redhaven' trees on seedling roots were used in these tests. Daminozide (400 ppm) was applied to 'Golden Delicious' and 'Staymared' trees 25 days after petal fall (APF). Ethephon (150 ppm) was applied to the 'Redhaven' trees 32 days APF. ABA (150 and 300 ppm) and DNP (500 ppm) were applied to apple leaves as dips (21). ¹⁴C-sucrose was applied by dipping leaves (2 basal full size leaves on shoots with 2 developing fruits) into a solution of Tween 20 (0.13%) and 50 μ Ci ¹⁴C-sucrose (0.043 mg) in 700 ml of water as soon as the above-applied materials had dried. Leaves dipped in the ¹⁴C-sucrose solution had deposits of ¹⁴C approximately 100 times greater than the amount translocated to the fruit, and there were no significant differences in ¹⁴C deposit on different treatments. The samples collected 24 or 48 hr after application of the ¹⁴C-sucrose were placed on dry ice and held at -20°C until lyophilized and ground for analysis. Five replicated samples of 4 fruit (2 from each of 2 terminals) were analyzed for each treatment. Samples were oxidized in a Harvey Biological oxidizer and counted in a liquid

scintillation spectrometer with an average of 84% efficiency.

In the shading test 'Red Rome' limbs were enclosed in bags of black floral shading cloth 23 days APF and were removed 7 days later. The tops of the bags were covered with white cheesecloth to avoid high temp in the bags. Fruit set was calculated from the numbers of fruit on shoots at time of treatment and after June drop. Water potential determinations were made on apple leaves 1 to 6 days after application of NAA using the method of Kaufman (10).

Results and Discussion

Daminozide reduced fruit set of 'Golden Delicious' but did not have a significant effect on 'Staymared' set (Table 1). However, 24 and 48 hr after treatment, the amount of ¹⁴C translocated to the fruit of each cultivar was significantly lower in trees sprayed with daminozide than in the untreated trees when compared on the basis of counts/min per 100 mg of lyophilized fruit tissue or on the basis of counts/min per fruit. Monselise and Luckwill (16) suggested the possibility that daminozide hinders translocation, especially acropetal translocation. Hicks and Brown (9) have shown that daminozide depressed the rate of ethylene evolution of apple leaves. Thus, apparently the mode of action of daminozide on fruit abscission is not through ethylene. In 'Staymared' the amount of metabolite available to the fruit, even though reduced by daminozide may have been adequate for the fruit to persist.

In our studies ethephon, which has been reported to reduce peach fruit set (26), reduced both fruit set and ¹⁴C translocation from leaves to fruit collected 24 or 48 hr after treatment (Table 1). Thus, with both 'Redhaven' peach and 'Golden Delicious' apple, sprays of growth substances which reduce metabolite translocation to fruit had a thinning effect.

Table 1. Effect of daminozide^z and/or ethephon^y on ¹⁴C translocation from foliage to fruit and on fruit retention of apple and peach.

Variable	Golden Delicious		Staymared		Redhaven	
	CK	Daminozide	CK	Daminozide	CK	Ethephon
% Fruit retained	63.3	48.9*	65	78.0 N.S.	79.4	54.7*
CPM/100 mg dry fruit tissue						
After 24 hr	243	119*	308	225*	80	65*
After 48 hr	418	209*	431	205*	182	66*

^z400 ppm applied 25 days APF.

^y150 ppm applied 32 days APF.

*Significantly different by students "t" test, 5% level.

N.S. Not significantly different.

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Table 2. Effect of ABA and DNP on ^{14}C -sucrose translocation^z to fruit^y.

Time of sampling (hr after treatment)	ABA (300 ppm)	ABA (150 ppm)	DNP (500 ppm)	Check
<i>Golden Delicious</i>				
24	116a	172b	83a	243c
48	189a	205a	270b	418c
<i>Staymared</i>				
24	114b	124b	41a	308c
48	172b	194b	74a	431c

^zCounts/min/per 100 mg dry fruit tissue.^yMean separation within rows by Duncan's multiple range test, 5% level.

Milborrow's (15) review article on ABA states that there was "... little doubt that ABA regulates the loss of a proportion of the young fruit ...". Both concn of ABA tested reduced ^{14}C translocation from foliage to fruit of both 'Golden Delicious' and 'Staymared' apples (Table 2). These data provide additional evidence that compounds that affect fruit abscission in some species also affect translocation of metabolites in apple. DNP reportedly inhibits sucrose translocation (8). Our orchard test with 'Staymared' and 'Golden Delicious' apple trees gave similar results (Table 2).

NAA and ethephon sprays are known to increase ethylene in plant tissue (11, 22). Some (19) have attributed the thinning effect of these chemicals to the increase in ethylene formation. The foregoing tests do not resolve the question of whether lack of metabolite or increased ethylene evolution is responsible for initiating abscission. Martin (12) has suggested that translocation is likely not the ultimate effect of a chemical thinner, although his schematic representation includes it as a possibility. His view could be correct for certain thinning materials but not necessarily for all, since our work (22, 23) suggests that a different mechanism apparently is involved in the thinning action of 1-naphthyl methylcarbamate and NAA.

To determine if reduced metabolite supply to fruitlets could initiate abscission in the absence of an exogenous chemical ethylene stimulant, 'Red Rome' apple limbs were enclosed in black cloth bags to largely eliminate endogenous metabolites and determine the effect on fruit set. When the bags were removed after 1 week none of the fruit on the enclosed limbs had abscised. They were noticeably smaller than control fruits but did not show symptoms typical of impending abscission. After the June drop, foliage appeared normal and the limbs could not be distinguished from check limbs. After the June drop the check limbs[had] retained 40.8% of the developing fruit and the enclosed limbs retained 5.4%.

Most of the few fruit retained by the enclosed limbs were on the most proximal lateral shoots, suggesting they received metabolites from nearby uncovered leaves as reported for grape (20). Apparently a reduction of metabolite supply available to developing apples can result in abscission without exogenous compounds that increase plant ethylene levels.

We have previously shown (22) that young-to-mature foliage enclosed in black cloth bags evolved less ethylene than leaves fully-exposed to light. Thus, ethylene levels in fruit or pedicel tissue of enclosed limbs were probably as low or lower than in tissue from exposed limbs, at least until reduced metabolites resulted in fruit senescence. The slow development of the abscission process of fruit on shaded limbs may be due to this initial low ethylene synthesis after enclosure whereas NAA sprays stimulate ethylene production within 2 days. These data support the premise that lack of metabolites rather than increased ethylene is the first step in NAA-induced abscission of young developing fruit.

Nomas (18) reported greater fruit thinning from an NAA

spray on shaded 'Satsuma' orange branches than on controls, and Moss's (17) recent report of reduced fruit set of 'Valencia' orange following application of a photosynthesis inhibitor further substantiates the importance of an adequate metabolite supply for retention of young developing fruit.

Flagging, a common response of apple trees to NAA sprays, is usually evident about 24 hr after application and persists for 7 to 10 days. Appearance suggests it might be due to wilting or epinasty. To determine if water stress was involved, leaf water potentials of untreated and NAA-sprayed 'Delicious' and 'Golden Delicious' leaves were compared. Flagging is not due to water stress since water potential of NAA-sprayed leaves of both cultivars was higher than that in the leaves from unsprayed trees for at least 4 days after NAA application (Table 3). The difference disappeared within 6 days. Less leaf flagging than normal was observed in this test, probably because the NAA was applied later in the season than usual, many shoots had started forming terminal buds and the tissue was more mature.

The increased water potential of leaves from NAA-sprayed trees could be a result of reduced transpiration owing to smaller stomatal aperture. This would reduce CO_2 diffusion into the leaf and, thus, photosynthesis. Bidwell and Turner's report (4) of increased photosynthesis following addition of indoleacetic acid (IAA) does not support this assumption. However, in their tests NAA did not affect photosynthesis, and they concluded that the effect of IAA is specific rather than a general effect of growth substances. Reduced photosynthesis may also reduce metabolite supply available to the developing fruit. Thus, NAA reduces translocation of exogenous ^{14}C -sucrose and apparently the supply of endogenous metabolites, resulting in reduced metabolites reaching the young fruit (23). This could be the reason for the slow growth of young apple fruits following an NAA spray (24). A slower rate of growth usually results in reduced synthesis of growth substances (3) which may explain the lower levels of growth substances in apple pedicel exudate reported by Crowe (6) and the depressed level of IAA in *Cleome* fruit following application of NAA (5). The reduced levels of metabolites and auxins occurred before the increase in ethylene following an NAA spray (22). The lower auxin level in the auxin-sprayed fruit presumably reduces the "sink" effect of the fruit, thereby further restricting its ability to compete for metabolites. This reduced rate of fruit growth and auxin level could result in a change in developing fruit from what Wareing and Phillips (27) call "condition 1" to "condition 2". Petioles in condition 1 are relatively insensitive to ethylene but in condition 2, when a measure of senescence has occurred, they are sensitive. Thus, the increased ethylene evolution within 48 hr after NAA treatment (22) could have a role in the abscission process after the reduced metabolite supply has changed the fruit from their condition 1 to condition 2. In a similar vein, Abeles et al. (1) point out that "... as long as functional quantities of auxin are present, no amount of ethylene can promote abscission." Thus the reduced levels of auxin in pedicel

Table 3. The effect of NAA^z on leaf water potential (bars) of 'Golden Delicious' and 'Delicious' apple leaves.

Time	Golden Delicious		Delicious	
	NAA	Check	NAA	Check
June 11 9:00 am	-7.5	-9.8*	-8.6	-10.9*
1:30 pm	-13.0	-15.9*	-13.5	-16.8*
June 12 7:30 am	-3.8	-5.1*	-4.6	-5.9*
June 14 8:30 am	-6.4	-9.2*	-6.0	-8.8*
June 16 8:30 am	-4.1	-4.0 ^y	-4.4	-4.1 ^y

^z25 ppm applied June 10, 1976.

*Difference in cultivar water potential significantly different at 5% level according to 'Students' "t" test.

^yNot significantly different.

exudate (5, 6) may be inadequate to inhibit ethylene promoted abscission especially after NAA has stimulated ethylene synthesis.

Application of TIBA to an apple pedicel, which reduces auxin translocation from fruit to abscission zone (11), results in fruit abscission (25). Abscission occurs even though TIBA reduces ethylene synthesis (2). Thus treatments using daminozide, or TIBA or shading, each of which apparently reduce ethylene evolution, can result in fruit abscission. This interpretation does not exclude ethylene as a factor in the abscission process but suggests that it functions after at least some senescence, perhaps due to the reduced auxin, has rendered the fruit susceptible to ethylene stimulation of abscission.

These data and that of other researchers indicate that a series of events, associated with fruit abscission, do in fact occur after an NAA spray, starting with a reduction of metabolites reaching the young fruit (21, 23) and followed sequentially by (a) reduced fruit growth (24), (b) reduced auxin in the fruit (5, 6), (c) increased ethylene synthesis (22), (d) initiation of the abscission process and (e) abscission of the fruit. Thus, apparently one preliminary screening test for potential apple thinning compounds may be based on their effects on ^{14}C -sucrose translocation from leaf to fruit.

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