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Effect of 6-benzylaminopurien; gibberellins A4+7; and N, N-dimethylamino succinamic acid on flowering and fruiting of 'Golden Delicious' apple trees.

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EFFECT OF 6-BENZYLAMINOPURINE; GIBBERELLINS A_{4+7}; AND N, N-DIMETHYLAMINO SUCCINAMIC ACID ON FLOWERING AND FRUITING OF 'GOLDEN DELICIOUS' APPLE TREES

A Thesis Presented

By

Joann Mary McLaughlin

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DEDICATION

Writing this thesis would not have been possible without the help of many different people. My close friends, my family, and of course BM all lended support through many trying moments. Ultimately, the real challenge and the work was mine and I, Joann Mary McLaughlin, have finally succeeded in the task.

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of 'Golden Delicious' Apple Trees

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Experiments were initiated on heavily blooming 'Golden Delicious' apple trees to determine the effect of and interactions among 6-benzylaminopurine (6-BA), gibberellins A4+7 (GA4+7), and n,n-dimethylamino succinamic acid (daminozide) on flower bud formation and the resultant vegetative and fruit effects. Repeat spray applications at full bloom (FB) +11 days through FB +61 days of 50 ppm 6-BA and/or 25 ppm of GA4+7 were made on limbs receiving 0 or 2000 ppm of daminozide and repeat spray applications at FB +4 through FB +57 days were made on limbs that had all flower clusters removed or all flower clusters retained. GA4+7 depressed flower bud formation, whereas, 6-BA not only increased bloom but also overcame some of the inhibitory effects of GA4+7 and seeded fruit on

flowering. Daminozide increased the effect of 6-BA on flowering when 6-BA and daminozide alone were marginally effective. 6-BA also increased lateral flower development in the blossom cluster and the number of 'king' flowers surviving mid-April cold temperatures regardless of crop load.

The effects of early applications of treatments on subsequent fruit characteristics were also examined. 6-BA increased russeting to undesirable levels and GA4+7 decreased it. 6-BA at the early application date increased fruit weight, length, and diameter. GA4+7 increased fruit length at both application starting dates but increased fruit weight only at the later application starting date. Daminozide reduced the effects of both 6-BA and GA4+7 on fruit length and diameter. Finally, GA4+7 decreased seed number and combined with 6-BA reduced seed number even more.

C H A P T E R I

INTRODUCTION

Plant hormones play an important role in flower initiation in apple trees. It has been suggested that all five classes of hormones may have either a direct or indirect role in flowering (63). However, attention has been focused mainly on gibberellins and only recently have cytokinins been considered as possibly an important regulator of flowering. Gibberellins applied exogenously depress flowering (70,75,94,110) and it is thought that gibberellins originating from developing seeds and young leaves will similarly depress flowering (48,64,81). Cytokinins have been reported to promote flowering in grape (87), some short day plants (7), and recently in apple (80,81). There is little information on the involvement of cytokinins in flowering and their interaction with gibberellins, thus it was thought a more detailed investigation should be initiated.

One reason the flowering process is a particularly important area for investigation in apple trees is because of the tendency to flower and fruit in alternate years. Flowers are formed in three locations on apple trees: terminally on long shoots, laterally on one-year-old shoots and terminally on shortened shoots or spurs. The cultivar 'Golden Delicious' was selected since it is a biennial bearer and is known to initiate flowers in all three locations. This makes it possible to study not only the involvement of cytokinins and

gibberellins in both the 'on' (cropping) and 'off' (forming flower buds) years of a biennial bearing cultivar but also to observe the effects on the different locations where flower buds are formed.

Flowering appears to be controlled on spurs by the presence of seeded fruit (12,70). Gibberellins, primarily gibberellins A4 and A7 (16), appear in the seeds about five weeks after full bloom and then peak at about nine weeks (48,64,81). Diffusion of gibberellins from the seed into the spur may prevent flower initiation (49). The presence of fruit on a spur in biennial cultivars usually eliminates flower bud formation on that spur. Although fruiting spurs contain higher levels of gibberellins than nonfruiting spurs (63,70), the peak in endogenous gibberellin levels from fruit diffusates does not correspond with a peak in fruiting spurs nor with the time of flower initiation (31,70).

The involvement of gibberellins in flowering of terminal and lateral buds is only circumstantial. Gibberellins are produced in young actively expanding leaves (61) and levels are found to be higher in longer shoots (75). Limited internode extension and early cessation of growth in nonfruiting spur buds suggest low levels of gibberellins are present. High levels of gibberellins being produced in rapidly growing shoots have been suggested to inhibit flowering in terminal and lateral buds of shoots (63). Application of gibberellins decreases flowering in lateral buds at concentrations as low as 30 ppm (70). Tromp (94) applied small quantities of gibberellins to the terminal tip and decreased flowering without

affecting shoot growth. However, Luckwill and Silva (66) found that the distribution of blossoming following gibberellin A3 treatment on 'Golden Delicious' differed from that following a heavy crop. Flowering was inhibited only on spurs and not terminally or laterally on shoots, whereas, following a heavy crop flowering was completely inhibited laterally on shoots and blossom clusters were formed mainly on spurs and occasionally terminally on long shoots.

In 1968, Luckwill (62) followed the concentration of cytokinins in the xylem sap of apple trees and showed that the levels were at a maximum at the time of full bloom and then fell when shoot growth ceased. He further proposed that flowering on shoots was regulated by a cytokinin/gibberellin ratio (63). Cytokinin levels had to be high at the time of shoot cessation when presumably gibberellin levels would be low in order for flower initiation to occur on shoots. Ramirez (81) found that cytokinins increased return bloom on spurs of annual bearing trees. He applied the cytokinins zeatin and 6-benzylaminopurine to deleafed, leafing, defruited, and fruiting spurs in the presence or absence of spray applications of daminozide. Both cytokinins increased return bloom even in the presence of fruit and increased the effect of leaves in promoting flowering.

Daminozide may reduce growth and increase return bloom on many different apple cultivars (5,22,107,110). Ramirez (81) found that daminozide enhanced the effect of cytokinins early in the season. It has been suggested that daminozide acts by suppressing gibberellin levels (19,46). Thus, spray applications of daminozide were included

and in combination with cytokinin and gibberellin sprays.

Regulation of flower bud formation, fruit set and other physiological responses may be affected by a promotor/inhibitor balance. This investigation was initiated to gain a better understanding of flower bud initiation in apple trees and to determine the degree of control exogenous growth regulator applications could have over flowering.

C H A P T E R II

LITERATURE REVIEW

The tendency for apple trees to bear fruit in alternate years (biennial bearing) has been recognized for centuries. Thus, there has been an interest in learning more about the physiological process of flower formation and how to control it for maximum production from year to year. Early work concentrated mainly on correlating different growth processes or the lack of them with flowering in the 'on' and 'off' years. Gourley (33) reported nonfruiting spurs had a larger leaf area than fruiting spurs and suggested that this aided flower formation by supplying more food reserves which were necessary for flower differentiation. Goff (32) was the first to note the time of flower bud differentiation and termination of shoot growth were related, in that flower bud differentiation occurred after shoot growth ceased for that year. However, Mack (65) reported that there was longer terminal growth in the 'off' year than the 'on' year which was confirmed by Tucker and Potter (97). Roberts (82) suggested the failure of buds to form flowers in the 'on' year was that shoots did not grow enough in length and diameter in the 'on' year. Other workers (33) stressd the importance of climatic factors such as rainfall and frost which were thought to be important in starting the biennial bearing pattern.

The emphasis in research changed after Kraus and Kraybill (54) found flowering in tomato was related to a high proportion of

carbohydrates to nitrogen (C/N ratio). Hooker (50) was the first to investigate this theory with apple trees, using fruiting and nonfruiting spurs and concluded that the starch to nitrogen ratio was a better index than the C/N ratio in apple trees. Harley et al (34) confirmed a relationship between high starch content and flower bud initiation and suggested two possible hypotheses: 1)that energy was required for flower bud differentiation which was supplied by starch, and/or; 2)that a specific hormone-like substance related to the synthesis of starch was produced in the leaves and moved to the regions of the spur where flowers were initiated. Girdling, ringing, or water stress were then thought to increase flowering by raising the carbohydrate to nitrogen ratio. However, after a detailed study of shoot growth, trunk thickening, root growth, and shoot, leaf, and spur development in the 'on' and 'off' years Singh (85) concluded that in the period from May to July 'off' year trees produce a greater amount of available leaf area per spur than 'on' year spurs and that this extra leaf area was responsible for flower bud differentiation and not changes in the carbohydrate to nitrogen ratio.

Davis (14) explained alterations in the C/N ratio and observed vegetative growth patterns as a consequence of flowering and not a cause since neither could be correlated as directly responsible for flower formation. Instead, the importance of plant hormones was emphasized and it was suggested flowering was dependent on the concentration of an unknown hormone. Tumanov (98) related inhibition

of flowering by the fruit with the seeds but it was not until Chan and Cain's report (12) that this inhibition was suggested to be a consequence of a hormone eminating from the seeds. Gibberellins were suggested to be the major source of inhibition since immature apple seeds contain large amounts (16) and exogenous applications were found to inhibit flowering (42,69). Fulford presented a series of papers relating anatomical events with flowering (26,27,28,29). He found that a steady plastochrone rate (the time interval between the inception of two successive leaf primordia) of seven days in nonbearing trees ensured that a minimum number of nodes were produced which was required before flower formation would occur. Fruit increased the plastochrone rate to 18 days so that this minimum number was not reached. Abbott (3) found in 'Cox's Orange Pippin' this number was 20 and in 'Golden Delicious' it was 16 (66). As a result, Fulford suggested that flower initiation would always occur unless it is otherwise inhibited.

Research efforts were then directed towards the gibberellins once inhibition of flowering appeared to be related to the seeds in the fruit and gibberellins. Dennis and Nitsch (16) identified gibberellins A4 and A7 as the main gibberellins in 'Golden Delicious' apple seeds. Luckwill (63,64) found gibberellin levels were higher in fruit bearing spurs than nonbearing spurs and that fruit of biennial bearing trees usually had a higher seed content than fruit of regular bearing trees. However, he found no evidence that seeds from biennial bearing trees contain more gibberellin than regular

bearing cultivars. Hoad (48) showed that more gibberellin-like activity was detected moving out of fruit of biennial bearing cultivars than from those that flower regularly even though these cultivars had similar seed numbers. Grochowska (40) found that almost all of the gibberellin and auxin present diffused from biennial bearing fruit while only half diffused from regular bearing cultivars.

Luckwill (63) proposed that flowering was influenced by the ratio of cytokinins to gibberellins based primarily on his work measuring cytokinin levels in the xylem sap of apple (62). He suggested (63) that cytokinins moving from the roots to the shoots must be sufficiently high and at the same time gibberellin levels from the shoots must be low enough to allow flower bud initiation. Following this various findings added indirect evidence not only for Luckwill's hypothesis but also for a more definitive involvement of cytokinins in the flowering process. Skene (84) increased the concentration of cytokinins in xylem exudate from cut grape stems after the growth retardant Cycocel (CCC) was added to the rooting medium suggesting the possibility that growth retardants may be increasing flowering by raising cytokinin levels and decreasing gibberellin levels. Chovjka et al (13) found bearing spurs treated with cytokinins resembled nonbearing spurs in certain metabolic activities such as nucleoprotein and phospholipid synthesis levels. Grochowska (41) found cytokinin increases in unpruned shoots in July coincided with the time of differentiation of flower buds and

suggested cytokinins were involved in differentiation. Srinivasan and Mullins (87) got increases in flower formation on grapes with cytokinins. They found flowering was dependent on repeated branching of undifferentiated primordia and that 6-benzylaminopurine applications increased flowering by increasing branching of the primordia resulting in increases in infloresence primordia. Hoad et al (47) found cytokinin levels were lower in grape leaves that subtended fruit suggesting that fruit may be affecting cytokinin metabolism and thus flowering. Ramirez and Hoad (80,81) got increases in spur return bloom on the annual bearing cultivar 'Cox's Orange Pippin' when zeatin alone, or combined with daminozide, was applied to to a cut petiole. Daminozide appeared to increase the effect of cytokinins on flowering particularly early in the season. Cytokinin levels in the xylem sap were not affected by daminozide application but there was an increase in levels in the seeds. Daminozide also caused a reduction in the rate of mitotic activity in the stem apex (also ref. 107).

Undoubtedly, cytokinins are involved in the flowering process. However, the exact role is unclear. In photoperiodic plants, it has been shown there is a series of induction events required prior to initiation of the meristem to a reproductive state (6). Bernier, Kinet, and Sachs (7) concluded that for all evocation events cytokinins appear to be most important in the release of buds from apical dominance, the increased rate of node production, and the increase in mitotic activity and synchronization of cells in the G1

phase of the mitotic cycle. Buban (9,10) has shown that with nonbearing apple spurs there are similarities in some of the required induction events with that of photoperiodic plants. How cytokinins fit in is unclear but as with gibberellins the answers may not be associated with changes in hormone levels. A current theory on hormone action (73,93), states that hormones are ubiquitous in all plants and hormone responses mirror changes in tissue sensitivity rather than changes in hormone levels.

C H A P T E R III

MATERIALS AND METHODS

Uniform 16 year old 'Golden Delicious' trees on Malling 7 (M7) rootstocks growing at the Horticulture Research Center in Belchertown, Massachusetts were selected. In 1980, the bloom was very heavy on all trees averaging 18 blossom clusters/cm of limb circumference.

Experiment 1. Effect of 6-Benzylaminopurine (6-BA), Gibberellins A4+7 (GA4+7), and N,N-Dimethylamino Succinamic acid (Daminozide) on Flowering and Fruiting of 'Golden Delicious'

Prior to bloom in 1980, uniform limbs 12 to 15 cm in diameter were selected on eighteen trees, their diameter measured and the total number of blossom clusters on each was counted. Trees were then grouped into nine pairs according to their bloom density and at full bloom (FB) +11 days one of each paired tree was sprayed to the drip point with 2000 ppm daminozide (as the Alar 85 formulation, Uniroyal Co., Naugatuct, Conneticut). On each of the eighteen trees four limbs were selected and randomly assigned to one of four treatments. One limb on each daminozide and untreated tree was sprayed to the drip point with 50 ppm of 6-BA, (as the ABG 3034 formulation, distributed by Abbott Laboratories, North Chicago, Ill.); a second with 25 ppm of GA4+7, (as the ABG 3035 formulation by Abbott Laboratories, North Chicago, Ill.), and a third limb received

both 50 ppm of 6-BA and 25 ppm of GA4+7. A fourth tagged limb on each tree was untreated and served as the check. The 6-BA and GA4+7 treatments were applied at FB +11, +20, +33, +45, and +61 days. Treatments were arranged as a completely randomized design with a split for the daminozide treatment.

Fruit set was determined after the 'June drop' period in July by counting the total number of persisting fruit on each tagged limb and then expressed on both a blossom cluster and limb circumference basis. Thirty fruit were harvested at maturity from each tagged limb. The weight, length, diameter, and the number of aborted and viable seeds were determined. Samples were evaluated at the same time for the severity of russeting based on a visual scale from 1 to 5 (over 50% of the fruit surface was russeted = 5, 40 to 50% = 4, 25 to 40% = 3, 10 to 25% = 2, and less than 10% = 1). After harvest, all of the leaves on each tagged limb were removed and the total leaf area was determined by a LiCor Model 3100 Area Meter. Terminal growth was measured on five shoots per tagged limb. Return bloom was determined on the same tagged limbs prior to full bloom in 1981. Fruit set was counted in 1981 at the completion of 'June drop' in July.

Experiments 2 and 3, Effect of 6-BA and GA4+7 on Fruiting and Nonfruiting Limbs of 'Golden Delicious'

Four limbs, 12 to 15 cm in diameter, on each of eight trees were selected and randomly assigned to one of the following treatments: a. all flower clusters retained (+ flowers), b. all flower clusters removed (- flowers), c. - flowers + 6-BA, d. + flowers + 6-BA. 6-BA was applied at 50 ppm at FB +4, +12, +27, +42 and +57 days. Treatments were arranged as a randomized complete block design with 8 replications.

Experiment 3 was designed the same as experiment 2 but 25 ppm of GA4+7 was applied instead of 6-BA at the same times after full bloom.

Thirty fruit were harvested at maturity from each tagged limb bearing fruit. The weight, length, diameter, and the number of aborted and viable seeds were determined for all harvested fruit. Samples were evaluated in the same manner as in experiment 1 for russeting. Terminal growth was measured on five shoots per tagged limb. Return bloom was counted on the same tagged limbs prior to full bloom in 1981. On twenty spur clusters per tagged limb blossom cluster quality was evaluated by counting the number of flowers in a cluster and the percent of the clusters with a viable 'king' flower. Fruit set was determined on the same tagged limbs in 1981 in the same manner.

In experiment 3, blossom quality in 1981 was evaluated only for treatments deflowered in 1980. Fruit were harvested again at

maturity in 1981 on limbs deflowered in 1980 and the weight, length, diameter, severity of russeting, and the number of aborted and viable seeds were determined.

C H A P T E R IV

RESULTS

Effect of 6-BA, GA4+7, and Daminozide on Flowering

Due to chance there was not a uniform bloom on all limbs prior to treatment application (Table 1). GA4+7 treated limbs had a heavier bloom. However, fruit set on these limbs was similar to check limbs after 'June drop'. 6-BA plus daminozide caused some fruit thinning whereas the GA4+7 plus daminozide combination increased fruit set.

Bloom in 1981 was greater on 6-BA treated limbs than the check or the 6-BA plus GA4+7 treatments (Table 2). Although daminozide did not increase bloom alone, when 6-BA or 6-BA plus GA4+7 were combined with daminozide there was greater flowering. GA4+7 reduced but did not eliminate the increase in flowering caused by 6-BA plus daminozide. GA4+7 alone or in combination with daminozide essentially eliminated flowering. This distorted and underestimated the error terms in the analysis of variance. Bartlett's test for homogenity of variance on the treatment means indicated there was not normal distribution of experimental error, an assumption that has to be met for an analysis of variance test to be done (88,105). Therefore, the two GA4+7 treatments with and without daminozide were omitted from return bloom and fruit set data for 1981 and the analysis of variance was repeated. There was no increase on fruit

Table 1. Effect of 6-benzyladenine (BA), gibberellin A_{4+7} (GA), and daminozide (D) on bloom and fruit set, 1980.

Treatments[z] (ppm)	Blossom clusters/cm limb circumference	Fruit/100 blossom clusters	Fruit/cm limb circumference[w]
1 Control	16.0a[y]	75.2a	11.9a
2 BA50	16.8a	64.3a	10.3a
3 GA25	21.0b	64.0a	13.2a
4 BA + GA25	18.1ab	75.9a	13.3a
5 Daminozide (D) 2000	17.3a[y]	76.9bc	13.1b
6 BA50 + D2000	16.5a	58.3a	9.6a
7 GA25 + D2000	19.7a	86.7c	16.9c
8 BA50 + GA5 + D2000	17.4a	66.1ab	11.3ab
Analysis of variance[x]			
Daminozide	NS	NS	NS
BA, GA	**	*	**
D, BA, GA interation	NS	*	NS
Significance[x]			
Trt 1 vs. Trt 5	NS	NS	NS
Trt 1 vs. Trt 7		NS	**
Trt 2 vs. Trt 6	NS	NS	NS
Trt 3 vs. Trt 7	NS	*	NS
Trt 4 vs. Trt 8	NS	NS	NS

[z]BA and GA were applied at Full Bloom (FB) + 11, + 20, + 33, + 47, and + 61 days. D was applied at FB + 11 days in 1980.

[y] Mean separation within split plot, (----), by Duncan's Multiple range Test, 5% level.

[x] Significant at the 5% (*) or 1% (**) level, or nonsignificant at the 5% level (NS).

[w] Analysis of variance and mean separation performed on transformed data via equation: F/LC80 = LN (F/LC80).

Table 2. Effect of 6-benzyladenine (BA), gibberellin A_{4+7} (GA) and daminozide (D) on bloom and fruit set, 1981.

Treatments[z] (ppm)	Blossom clusters/cm limb circumference[w]	Flowering spurs (%)[w]	Fruit/100 blossom clusters[w]	Fruit/cm limb circumference[w]
1 Control	.59a[y]	4.69a	51.0a	.51a
2 BA50	1.35b	8.25a	110.0b	1.62b
3 GA25	.04	.29	14.8	.04
4 BA50 + GA25	.38a	2.76a	111.5b	.58a
5 Daminozide (D)2000	1.17a[y]	8.51a	96.4a	.94a
6 BA50 + D2000	4.46c	27.35b	95.3a	3.25c
7 GA25 + D2000	.08	1.07	39.7	.15
8 BA50 + GA25 + D2000	2.31b	12.43a	110.5a	1.93b
Analysis of variance[x]				
Daminozide (D)	**	**	NS	**
BA, BA + GA	**	**	*	**
D + BA, GA interaction	*	NS	NS	NS
Significance[x]				
Trt 1 vs. Trt 5	NS	NS	*	*
Trt 2 vs. Trt 6	**	**	NS	**
Trt 4 vs. Trt 8	**	**	NS	**

z BA and GA were applied at Full Bloom (FB) + 11, + 20, + 33,+ 47, and + 61 days. D was applied at FB + 11 days in 1980.

y Mean separation within split plot, (----), by Duncan's Multiple Range Test, 5% level.

x Significant at the 5% (*) or 1% (**) level or nonsignificant at the 5% level (NS).

w Analysis of variance and mean separation preformed on transformed data via following equations: BCLC81 = LN(BCLC81 + .5), % Bloom = ARCSIN (SQRT (% Bloom/54), F/LC81 = LN (F/LC81 + .5). Treatments 3 and 7 were not included.

bearing spurs without daminozide. Bloom on spurs was greater on 6-BA plus daminozide limbs than 6-BA or daminozide alone. 6-BA plus daminozide could not overcome the inhibitory effects of GA4+7 sprays. Treatments that increased bloom also increased fruit set in 1981 based on a limb circumference basis. Only 6-BA or 6-BA plus GA4+7 increased fruit set when expressed on a blossom cluster basis.

Daminozide had no influence on the increased leaf area caused by 6-BA plus GA4+7 (Table 3). Neither 6-BA nor GA4+7 alone increased leaf area. However, when 6-BA and GA4+7 were combined leaf area was increased either with or without daminozide. GA4+7 alone increased terminal growth but when combined with daminozide there was no growth stimulation.

Effect of 6-BA and GA4+7 on Flowering of Fruiting and Nonfruiting limbs

Bloom and fruit set were not recorded in 1980 in these two experiments due to the removal of all flowers from two of the treatments. The remaining limbs had a very heavy crop load similar to the value of 16.0 blossom clusters/ cm of limb circumference on untreated limbs of trees in Experiment 1.

6-BA failed to influence return bloom or fruit set on nonfruiting limbs but it did result in a substantial increase in bloom and fruit set on fruiting limbs (Table 4). The presence of fruit decreased return bloom and subsequent fruit set whether or not 6-BA was applied.

Table 3. Effect of 6-benzyladenine (BA), gibberellin A_{4+7} (GA), and daminozide (D) on vegetative characteristics in 1980.

Treatments[z] (ppm)	Leaf area/leaf (cm^2)	Terminal growth (cm)
1 Control	14.85a[y]	13.5ab
2 BA50	15.49a	12.9a
3 GA25	15.31a	18.4b
4 BA50 + GA25	17.53b	15.5ab
5 Daminozide (D)2000	15.87a[y]	15.9a
6 BA50 + D2000	17.09ab	15.1a
7 GA25 + D2000	16.48ab	15.3a
8 BA50 + GA25 + D2000	17.99b	14.8a
Analysis of variance[x]		
Daminozide (D)	NS	NS
BA, GA	*	NS
D + BA, GA interaction	NS	NS
Significance[x]		
Trt 1 vs. Trt 5	NS	NS
Trt 2 vs. Trt 6	NS	NS
Trt 3 vs. Trt 7	NS	NS
Trt 4 vs. Trt 8	NS	NS

z BA and GA were applied at Full Bloom (FB) + 11, + 20, + 33, + 47 and + 61 days. D was applied at FB + 11 days in 1980.

ý Mean separation within split plot,(----), by Duncan's Multiple Range Test, 5% level.

x Significant at the 5% (*) or 1% (**) level, or nonsignificant at the 5% level (NS).

Table 4. Effect of 6-benzyladenine (BA) on bloom and fruit set of fruiting and nonfruiting limbs, 1981.

Treatments[z] (ppm)	Blossom clusters/cm limb circumference[y]	Flowering spurs (%)[y]	Fruit/100 blossom clusters[y]	Fruit/cm limb circumference[y]
1 + Flowers - BA	.9	3.6	5.6	.1
2 - Flowers - BA	13.4	52.0	40.7	5.6
3 - Flowers + BA50	13.6	59.3	50.7	6.0
4 + Flowers + BA50	3.8	19.6	33.6	1.2
Analysis of variance[x]				
Treatments	**	**	**	**
Significance[x]				
Trt 1 vs. Trt 4	**	**	**	**
Trt 3 vs. Trt 4	**	**	*	
Trt 2 vs. Trt 3	NS	NS	NS	NS
Trt 2 vs. Trt 4			**	

z Flowers removed at Full Bloom (FB). BA was applied at FB + 4, + 12, + 26, + 42 and + 57 days in 1980.

y Analysis of variance and mean separation procedure performed on transformed data via equations: BC LC 81 = LN (BCLC 81 + .5), % Bloom = ARCSIN (SQRT (% Bloom/90)), F/LC 81 = LN (F/LC 81 + .5).

x Significant at the 5% (*) or 1% (**) level, or nonsignificant at the 5% level (NS).

On April 15th, 20th, and 21st, there were -2.8 C (27 F), -2.8 C (27 F), and -2.2 F (28 F) temperatures that had been preceeded by above normal temperatures in early-mid April at the Horticulture Research Center that resulted in death to many 'king' flowers. 6-BA substantially increased the number of 'king' flowers surviving the cold temperatures regardless of crop load (Table 5). 6-BA increased the number of flowers in a cluster. Crop load had little influence on the number of flowers in the cluster or the % viable 'king' flowers. The improved spur quality may have been a factor in the subsequent increase in fruit set (Table 4). Only crop load decreased terminal growth.

The combination of a heavy crop and GA4+7 treatment (+ flowers +GA4+7), completely inhibited flower initiation in 1980 eliminating return bloom and fruit set in 1981 (Table 6). As in Experiment 1, including this treatment falsely underestimated the error term so it was omitted and the analysis of variance was repeated.

The presence of fruit essentially eliminated return bloom (Table 6). GA4+7 had no influence on return bloom and fruit set on deflowered limbs. The number of flowers/spur, the % viable 'king' flowers, and terminal growth were not affected by GA4+7 treatment (Table 7).

Table 5. Effect of 6-benzyladenine (BA) on terminal growth, 1980 and blossom quality, 1981 of fruiting and nonfruiting limbs.

Treatment (ppm)	Terminal growth (cm)	# Flowers/spur clusters	Viable king flowers (%)
1 + Flowers - BA	26.0	2.9	21.8
2 - Flowers - BA	32.0	3.2	39.1
3 - Flowers + BA50	35.0	4.0	58.1
4 + Flowers + BA50	31.2	3.3	55.0
Analysis of variance			
Treatments	*	**	**
Significance			
Trt 1 vs. Trt 4	NS	*	**
Trt 1 vs. Trt 3	**		
Trt 1 vs. Trt 2	NS	NS	*
Trt 2 vs. Trt 3		**	*
Trt 3 vs. Trt 4		**	NS
Trt 1 and 2 vs. Trt 3 and 4		**	**
Trt 1 and 4 vs. Trt 2 and 3		**	NS

[z] Flowers removed at Full Bloom (FB). BA was applied at FB + 4, + 12, + 26, + 42, and + 57 days in 1980.

[y] Significant at the 5% (*) or 1% (**), or nonsignificant at the 5% level (NS).

Table 6. Effect of gibberellin A_{4+7} (GA) on bloom and fruit set of fruiting and nonfruiting limbs, 1981.

Treatments[z] (ppm)	Blossom clusters/cm limb circumference[y]	Flowering spurs (%)[y]	Fruit/100 blossom clusters[y]	Fruit/cm limb circumference[y]
1 + Flowers - GA	.3	2.1	42.0	.1
2 - Flowers - GA	10.7	56.6	60.7	5.9
3 - Flowers + GA25	8.3	38.1	65.0	4.6
4 + Flowers + GA25	0.0	0.0	0.0	0.0
Analysis of variance[x]				
Treatments	**	**	NS	**
Significance[x]				
Trt 1 vs. trt 2	**	**	NS	
Trt 2 vs. trt 3	NS	NS	NS	NS
Trt 1 vs. trt 3			**	

z Flowers were removed at Full Bloom (FB). GA was applied at FB + 4, + 12, + 26, + 42 and + 57 days in 1980.

y Significant at the 5% (*) or 1% (**) level, or nonsignificant at the 5% level (NS).

x Analysis of variance and mean separation procedure performed on transformed data via equation: BCLC81 = LN(BC LC81 + .5), % Bloom = ARCSIN (SQRT (% Bloom/85)). Treatment 4 was not included.

Table 7. Effect of gibberellin A_{4+7} (GA) on terminal growth, 1980 and blossom quality, 1981 of fruiting and nonfruiting limbs.

Treatments[z] (ppm)	Terminal growth (cm)	# Flowers/blossom cluster	Viable king flowers (%)
1 + Flowers - GA	29.1		
2 - Flowers - GA	30.6	3.6	47.5
3 - Flowers + GA25	29.1	3.4	61.3
4 + Flowers + GA25	31.2		
Analysis of variance[y]			
Treatments	NS	NS	NS

[z]Flowers removed at Full Bloom (FB). GA was applied at FB + 4, + 12, + 26, + 42 and + 57 days in 1980.

[y]Nonsignificant at the 5% level (NS).

Effect of 6-BA, GA4+7, and Daminozide on Fruiting

6-BA increased the severity of russeting whereas GA4+7 decreased it (Table 8). GA4+7 reduced the 6-BA increase in russeting to check levels. Daminozide had no influence on russeting or fruit weight. 6-BA and GA4+7 alone or 6-BA plus daminozide increased fruit weight.

The L/D ratio was increased by the GA4+7 treatment and when combined with 6-BA there was a further increase (Table 9). There was a comparable increase in the L/D ratio on the GA4+7 and GA4+7 plus 6-BA treated fruit when daminozide was added. GA4+7 alone or when combined with 6-BA increased fruit length whereas 6-BA increased fruit length only when combined with daminozide and only in comparison to daminozide treated fruit. Fruit diameter was reduced when 6-BA and GA4+7 were combined and all daminozide treatments except 6-BA plus GA4+7. GA4+7 alone or plus daminozide increased the number of aborted seeds and lowered the number of viable seeds (Table 10). 6-BA had no influence on aborted or viable seed number but when combined with GA4+7 there was a synergistic increase in aborted seeds and a corresponding decrease in viable seed number. Daminozide did not influence seed number.

Effect of 6-BA and GA4+7 on Fruiting

Fruit were collected from only two treatments due to flower removal in the spring of 1980 on the remaining treatments. In 1981,

Table 8. Effect of 6-benzyladenine (BA), gibberellin A_{4+7} (GA) and daminozide (D) on russeting and fruit weight, 1980.

Treatments[z] (ppm)	Russeting[y]	Fruit weight/fruit (gms)
1 Control	2.7b[x]	97.0b
2 BA50	3.4a	112.0a
3 GA25	2.0c	109.0a
4 BA50 + GA25	2.5b	105.0ab
5 Daminozide (D)2000	3.1b[x]	94.0b
6 BA50 + D2000	3.5a	105.0a
7 GA25 + D2000	1.9c	95.0b
8 BA50 + GA25 + D2000	2.3d	103.0ab
Analysis of variance[w]		
Daminozide (D)	NS	NS
BA, GA	**	**
D, BA, GA interaction	NS	NS
Significance[w]		
Trt 1 vs. Trt 5	NS	NS
Trt 2 vs. Trt 6	NS	NS
Trt 3 vs. Trt 7	NS	*
Trt 4 vs. Trt 8	NS	NS

[z] BA and GA were applied at Full Bloom (FB) + 11, + 20, + 33, + 47, and + 61 days. D was applied at FB + 11 days in 1980.

[y] Scale 5 = over 50%; 4 = 40 to 50%; 3 = 25 to 40%; 2 = 10 to 25%; 1 = less than 10%.

[x] Mean separation within split plot, (----), by Duncan's Multiple Range Test, 5% level.

[w] Significant at the 5% (*) or 1% (**) level, or nonsignificant at the 5% level (NS).

Table 9. Effect of 6-benzyladenine (BA), gibberellin A_{4+7} (GA) and daminozide (D) on the L/D ratio, fruit length, and fruit diameter, 1980.

Treatments[z] (ppm)	Length/diameter L/D	Fruit length/ fruit (cm)	Fruit diameter/ fruit (cm)
1 Control	.926a[y]	5.75a	6.21b
2 BA50	.931a	5.87ab	6.31b
3 GA25	.965b	5.99b	6.21b
4 BA50 + GA25	.980c	5.93b	6.05a
5 Daminozide (D)2000	.930a[y]	5.47a	5.88a
6 BA50 + D2000	.936a	5.66b	6.05b
7 GA25 + D2000	.961b	5.65b	5.88a
8 BA50 + GA25 + D2000	.970b	5.82b	5.99ab
Analysis of variance[x]			
Daminozide (D)	NS	*	**
BA, GA	**	**	*
D, BA, GA interaction	NS	NS	*
Significance[x]			
Trt 1 vs. Trt 5	NS	*	**
Trt 2 vs. Trt 6	NS	NS	*
Trt 3 vs. Trt 7	NS	**	**
Trt 4 vs. Trt 8	NS	NS	NS

z BA, GA applied at Full Bloom (FB) + 11, +20, +33, +47, + 61 days in 1980. D was applied at FB + 11 days in 1980.

y Mean Separation within split plot, (----), by Duncan's Multiple Range Test, 5% level.

x Significant at the 5% (*) or 1% (**) level, or nonsignificant at the 5% level (NS).

Table 10. Effects of 6-benzyladenine (BA), gibberellin A_{4+7} (GA) and daminozide (D) on seed number, 1980.

Treatments[z] (ppm)	Aborted seeds/ fruit[y]	Viable seeds/ fruit	Total seeds/ fruit
1 Control	.4a[x]	8.1c	8.4a
2 BA50	.8b	8.0c	8.8ab
3 GA25	2.0c	6.4b	8.4a
4 BA50 + GA25	4.0d	5.0a	9.0b
5 Daminozide (D)2000	.3a[x]	8.2c	8.5a
6 BA50 + D2000	.6a	7.7c	8.4a
7 GA25 + D2000	1.6b	7.0b	8.6a
8 BA50 + GA25 + D2000	3.6c	4.8a	8.4a
Analysis of variance[w]			
Daminozide (D)	NS	NS	NS
BA, GA	**	**	NS
D, BA, GA interaction	NS	NS	NS
Significance[w]			
Trt 1 vs. Trt 5	NS	NS	NS
Trt 2 vs. Trt 6	NS	NS	NS
Trt 3 vs. Trt 7	NS	NS	NS
Trt 4 vs. Trt 8	NS	NS	NS

z BA and GA were applied at Full Bloom (FB) + 11, + 20, + 33, + 47, and + 61 days. D was applied at FB + 11 days in 1980.

y Analysis of variance and mean separation procedure performed on transformed data via equation: # aborted = LN (# Aborted + .5).

x Mean separation within split plot by Duncan's Multiple Range Test, 5% level.

w Significant at the 5% (*) or 1% (**), or nonsignificant at the 5 level (NS).

fruit were collected from the two treatments of the GA4+7 experiment that were deflowered in 1980.

6-BA increased the severity of russeting, fruit weight, L/D ratio, fruit length, and fruit diameter (Table 11). 6-BA had no influence on seed number (Table 12).

GA4+7 reduced the severity of russeting in 1980 but not in 1981 (Table 13). GA4+7 increased fruit weight in 1981 but not in 1980. The L/D ratio was increased in 1980 by an increase in fruit length (Table 14). GA4+7 had no carryover effect in 1981. There was an increase in aborted seed number by GA4+7 in 1980 but not in 1981 (Table 15). GA4+7 had no influence on viable or total seed number.

Statistical Analysis of Data

Bartlett's test was done on each variable in all three experiments to determine if transformation of the data were necessary. Logarithmic or arcsin transformations were utilized (105), and the analysis of variance and mean separation procedure was repeated with the transformed data. In Experiment 1, treatment means within the split plot of daminozide were separated by Duncan's multiple range test at the 5% level using the whole plot error term. Comparisons of daminozide and non-daminozide treatments were made with single degree of freedom t tests using a pooled split and whole plot error term with a tabulated t value (88). In Experiments 2 and 3, comparisons were made with single degree of freedom f tests.

Table 11. Effect of 6-benzyladenine (BA) on fruit characteristics in 1980.

Treatments[z]	Russeting[y]	Fruit weight/ fruit (gms)	Length/diameter L/D	Fruit length/ fruit (cm)	Fruit diameter/ fruit (cm)
+ Flowers - BA50	2.7	117.0	.936	6.04	6.45
+ Flowers + BA50	3.4**[x]	136.0*	.974**	6.57**	6.75*

z
BA was applied at Full Bloom (FB) + 4, + 12, + 26, + 42, and + 57 days in 1980.

y
Scale 5 = over 50%; 4 = 40 to 50%; 3 = 25 to 40%; 2 = 10 to 25%; 1 = less than 10%

x
Significant at the 5% (*) or 1% (**) level.

Table 12. Effect of 6-benzyladenine (6-BA) on seed number in 1980.

Treatments[z] (ppm)	Aborted seeds/ fruit	Viable seeds/ fruit	Total seeds/ fruit
+ Flowers - BA50	.4	8.2	8.6
+ Flowers + BA50	.5 NS[y]	7.5 NS	8.0 NS

[z] BA was applied at Full Bloom (FB) + 4, + 12, + 26, + 42, and + 57 days in 1980.

[y] Nonsignificant (NS) at the 5% level.

Table 13. Effect of gibberellin A_{4+7} (GA) on fruit characteristics in 1980 and 1981.

Treatments[z] (ppm)	Russeting[y]		Fruit weight/fruit (gms)	
	1980	1981	1980	1981
+ Flowers - GA25	2.6	2.5	119.0	143.0
+ Flowers + GA25	2.0**[x]	2.3 NS	121.0 NS	154.0*

z GA was applied at Full Bloom (FB) + 4, + 12, + 26, + 42 and + 57 days in 1980.

y Scale 5 = over 50%; 4 = 40 to 50%; 3 = 25 to 40%; 2 = 10 to 25%; 1 = less than 10%.

x Significant at the 5% (*) or 1%(**), or nonsignificant at the 5% level (NS).

Table 14. Effect of gibberellin A_{4+7} (GA) on the L/D ratio, fruit length, and fruit diameter in 1980 and 1981.

Treatments[z] (ppm)	Length/diameter		Fruit length/fruit (cm)		Fruit diameter/fruit (cm)	
	1980	1981	1980	1981	1980	1981
+ Flowers - GA25	.929	.952	5.93	6.55	6.42	6.88
+ Flowers + GA25	.963**[y]	.941 NS	6.24*	6.56 NS	6.48 NS	6.96 NS

[z] GA was applied at Full Bloom (FB) + 4, + 12, + 26, + 42, and + 57 days in 1980.

[y] Significant at the 5% (*) level or 1% (**) level, or nonsignificant at the 5% level (NS).

Table 15. Effect of gibberellin A_{4+7} (GA) on seed number in 1980 and 1981.

Treatments[z] (ppm)	Aborted seeds/fruit 1980	Aborted seeds/fruit 1981	Viable seeds/fruit 1980	Viable seeds/fruit 1981	Total seeds/fruit 1980	Total seeds/fruit 1981
+ Flowers - GA25	.4	.6	8.3	7.2	8.7	7.8
+ Flowers + GA25	1.3**[y]	.7 NS	7.0 NS	7.1 NS	8.2 NS	7.8 NS

[z] GA was applied at Full Bloom (FB) + 4, + 12, + 26, + 42, and + 57 days in 1980.

[y] Significant at the 1% (**) level or nonsignificant (NS) at the 5% level.

C H A P T E R V

DISCUSSION

Effect of 6-BA, GA4+7, and Daminozide on Flowering

Limbs were not totally uniform in bloom prior to growth regulator treatments (Table 1), thus it is unclear whether fruit set was a reflection of bloom density, spray application, or a combination of both. It is known that heavily blooming trees will usually have a larger 'June drop' than lighter blooming trees (111,112), so that GA4+7 treated limbs which had a heavier bloom before spray application may have had a larger 'June drop' and thus final fruit set would be similar to untreated and 6-BA treated limbs (Table 1). Bloom and fruit set were similar to the check on limbs receiving 6-BA and 6-BA plus GA4+7 treatments. Therefore, it would appear these treatments did not affect final fruit set.

Final fruit set was affected differently when 6-BA or GA4+7 were combined with daminozide. 6-BA plus daminozide thinned, GA4+7 increased set on a limb area basis, and 6-BA plus GA4+7 plus daminozide had no effect on fruit set (Table 1). Interactions of either 6-BA or GA4+7 with daminozide on fruit set are not well documented in the literature. GA4+7 has been reported to increase fruit set by increasing initial fruit set (15) and by retarding 'June drop' through a 50 ppm FB +23 day treatment on 'Golden Delicious'. Greene et al (36) reported that on 'McIntosh' GA4+7 plus daminozide

may have enhanced fruit set. Martin et al (72) reported increases in fruit set with 500 ppm of cytokinins applied at petal fall +3 days, but it was not confirmed the following year. There are no other reports that 6-BA alone influences fruit set although when combined with GA4+7 reductions in set have been observed with 'Delicious' (99). Daminozide alone may have no effect on fruit set (5) (Table 1) or may increase set (23). Thus, it is unclear whether the effects on fruit set with GA4+7 and 6-BA are a result of an interaction with daminozide, or a result of an increase in absorption of either 6-BA or GA4+7 when daminozide was applied due to the addition of a surfactant in the daminozide formulation.

Elevated ethylene levels in flowers or developing fruit have been found following treatments that reduce set (34) and following chemical thinner application (102) suggesting that ethylene may be involved in fruit set. A reduction in fruit set was found when 6-BA plus daminozide were applied (Table 1). Both 6-BA and GA4+7 have been reported to increase ethylene levels (4), but not to the levels of chemical thinners such as ethephon and napthalenectic acid (102), so it is unlikely GA4+7 when combined with daminozide reduced ethylene levels resulting in an increase in set. Therefore, fruit set results cannot be explained solely on the basis of increases or decreases in ethylene levels.

Treatments should have comparable fruit set values with a check to determine if bloom was increased or decreased independently of a fruit thinning effect, since an increase in return bloom will usually

accompany a reduction in fruit set (44). All treatments except 6-BA plus daminozide had similar fruit set values in 1980 (Table 1). Thus, the increases in bloom were probably a direct result of spray treatment (Table 2). 6-BA plus daminozide limbs were comparable to 6-BA limbs in fruit set (Table 1), but the degree of blossoming was greater than 6-BA treatments (Table 2). Even though 6-BA plus daminozide reduced set, increases in bloom were larger than can be explained by fruit thinning effects, thus increased flowering is most likely a result of a direct response of the spray treatment on flowering.

When spray applications started at FB +4 days, 6-BA increased both spur return bloom and total bloom on fruiting limbs as expressed on a blossom cluster/cm of limb circumference basis (Table 4). However, 6-BA had no effect on nonfruiting limbs. Spray applications of 6-BA starting at FB +11 days increased only total bloom (Table 2). Terminal and lateral bloom were not measured separately but spur bloom was so that total bloom would be a measurement of spur, terminal, and lateral bloom. Thus, increases in total bloom could have been a result of small increases in spur, terminal, and lateral bloom or direct increases in terminal or lateral bloom. However, following a heavy crop lateral bloom is usually inhibited and flowering is mainly on spurs and occasionally terminally on shoots (65). This was observed visually. Since spur bloom alone was not increased by 6-BA applications starting at FB +11 days total bloom increases were probably a result of small increases in both terminal

and spur bloom. By FB +11 days flowering may then be inhibited on spurs so that increases were no longer significant and thus applications at that date were not as effective at increasing spur bloom as applications starting at FB +4 days.

When applied at FB +11 days, 2000 ppm of daminozide had no effect on total or spur bloom (Table 2). Since daminozide aids return bloom on regular bearing trees at that concentration and during that time period (5,35,66), it would seem the heavy crop reduced the effectiveness of daminozide. Both 6-BA and daminozide then have the capacity to increase flowering under the right conditions. Combined 6-BA and daminozide synergisticly increase both spur and total bloom (Table 2). It has been suggested that daminozide increases flowering indirectly by reducing gibberellin levels from the fruit (19,46), but so far this has not been proven experimentally (81). There is little information available indicating how 6-BA and other cytokinins or cytokinins and daminozide increase flowering on apple trees (79,80).

Fulford (28) suggested that flower initiation will occur unless it is otherwise inhibited and the inhibitory effect on spurs was due to the presence of seeded fruit. Inhibition by the fruit (or seeds) of flower initiation may be related to alterations in the metabolism of the spur and surrounding tissue, especially in biennial bearing cultivars. Starch levels are lower (38), the respiration rate of the leaves is higher (39), and the plastochrone rate (time interval between successive initiation of leaf primordia) is increased to

eighteen days indicating there is a general inhibition of cell division and a reduction in the strength of the apical meristem (29). Marino and Greene (70) found that inhibition of flowering on a biennial bearing cultivar started very early in the season and increased from that time onward. The start and the degree of inhibition appeared dependent on crop load. One way growth regulators may be effective at increasing flowering is partially through their ability to overcome enough of the alterations fruit are causing in the metabolic processes of the spur so that flower initiation will proceed. Chvojka et al (13) found levels of synthesis of nucleoproteins and phospholipids in fruiting spurs resembled nonbearing spurs after kinetin treatment. Grochowska (38) found daminozide was able to increase the starch content of fruiting spurs to similar levels as found in nonfruiting spurs. Changes in starch content, respiration rates, nucleoprotein and phospholipid synthesis levels are just a few of the indications that fruit are redirecting the metabolism in the spur and the apical meristem. If severe enough it may lead to the increase in the plastochrone rate. Buban (10) has suggested there are certain key cytochemical events such as an increase in RNA and DNA synthesis and a rise in the mitotic index which are required prior to flower initiation. A reduction in the strength of the apical meristem may then prevent these induction events from occurring.

6-BA and daminozide alone may not have been very effective at increasing bloom when applied at FB +11 days because inhibition by

seeded fruit was already too great to overcome. Earlier applications at FB +4 days and combinations with the growth retardant, daminozide, appear to be much more successful at countering the influence of seeded fruit. Daminozide, since it is not a natural hormone probably increases return bloom by partially overcoming some of the effects of seeded fruit on the spur's metabolism instead of a direct stimulation of the flowering process. Whether this is actually by reducing gibberellin levels (46), blocking interconversions of different gibberellins (55), inhibiting a specific action of the fruit, or by altering or affecting other hormone levels such as auxin (51,52) is not known at this time. Cytokinins however, may be involved not only in directly stimulating the flowering process but also in counteracting some of the inhibitory effects of seeded fruit. Cytokinins are important in early development when cell division is actively occurring (75) and in some of the induction events in the flowering process of photoperiodic plants such as the increase in mitotic activity and synchronization of cells in the G1 phase of the mitotic cycle (7). Whether this indicates the increases in flowering with 6-BA were a result of supplementing endogenous levels of cytokinins which the large volume of seeded fruit may have utilized, or that fruit may have changed tissue sensitivity in the spur so that cytokinins although present may be immobile or ineffective and exogenous applications were needed, or that exogenous applications may be directly stimulating some of the required cytochemical changes and helping to maintain the strength of the apical meristem and a

certain level of cell division activity, or whether exogenous 6-BA applications are partially overcoming some of the inhibitory effects of seeded fruit on the metabolism of the spur is also not known at this also time.

Three of the GA4+7 treatments had to be omitted (from experiments 1 and 3, Tables 2 and 6) because the combination of spray treatment and heavy crop nearly eliminated bloom and fruit set in 1981. The addition of GA4+7 to treatments that increased bloom reduced flowering in comparison to treatments without it (Table 2). GA4+7 applications at the same concentration on nonfruiting limbs had no effect (Table 6). Fulford (30) found a similar result on 'Sunset' apple trees. GA3 applications inhibited flowering but had no effect on trees that had been deblossomed even at concentrations as high as 5000 ppm suggesting inhibition of flowering is a result of an interaction between GA sprays and the fruit and that exogenous applications of GA further reinforce the inhibitory effect of fruit. Thus, on trees with a heavy crop, as in this investigation only low concentrations of GA4+7 were necessary to influence flowering.

Efforts to correlate GA4+7 diffusion peaks with high levels in the spur and the actual time of flower initiation have not proved successful (31,70), even though it is generally regarded that GA4+7 from the fruit is the source of inhibition of flowering (48,49,63,64). This has raised the question of whether it is the peak of GA activity which influences flowering or GA levels at an earlier date. Inhibition of flowering appeared to start very early

in the season in this investigation which Marino (70) found was a result of the heavy crop. GA4+7 sprays were effective at reducing flowering which Fulford (31) suggested was a result of supplementing the action of the fruit. 6-BA and daminozide were found to reduce the ability of the fruit to inhibit flowering and when GA4+7 was added this effect was partially reversed. The degree of inhibition of flowering then may be dependent not only on fruit load and thus GA levels but also on the concentration(s) of other hormone(s) in the spur. Seeded fruit inhibit flowering prior to the actual flower formation period, thus GA4+7 inhibition may not be associated with the actual transition of the meristem from a vegetative to a reproductive state.

Both leaf area and terminal growth appeared to be influenced more by the presence of a large crop than by growth regulator treatment (Table 3). Daminozide alone had no effect on area per leaf and did not interact with either 6-BA or GA4+7, which did not influence leaf area unless combined. Cytokinins and gibberellins are both important in cell division and enlargement (61,76) and thus in leaf development. Total leaf area on 'off' year trees is usually 2 to 3 times larger than in the 'on' year (56). Gibberellins have been found to increase terminal growth (75,94). Applications of both 6-BA and GA4+7 may then have been at too low a concentration to affect either the area per leaf or terminal growth.

Flower cluster number was increased on both fruiting and nonfruiting limbs by 6-BA applications (Table 5). GA4+7 applications

did not influence flower cluster number on nonfruiting limbs (Table 7) and on fruiting limbs cluster number was not counted since there were too few flowers to give an accurate representation. The king flower was included when the number of flowers/spur cluster were counted even though in some cases it had abscised due to cold damage. The increase in flower cluster number on nonfruiting limbs with 6-BA was particularly striking considering there was no effect on bloom (Table 4). Differentiation of the floral primordia is actually thought to begin in the lateral meristems of the infloresence but the terminal or 'king' flower soon begins to develop faster and overtakes the lateral flowers (28). Thus, fewer flowers per cluster would mean some of the lateral flowers had failed to develop. By applying 6-BA flower cluster number was increased indicating lateral flower development was enhanced. Kender and Carpenter (53) and Williams and Stahly (108) reported increases in lateral vegetative bud development with 6-BA, so it is not surprising reproductive bud development may also be increased. There is the possibility that the lower flower cluster number may be a result of a cytokinin deficiency. Luckwill and Whyte (62) found after bloom cytokinin levels in the xylem sap begin dropping and by the end of July levels are practically zero. Fruit seemed to partially negate 6-BA's influence on flower cluster number since fruiting limbs treated with 6-BA had a lower cluster number than nonfruiting limbs treated with 6-BA, although there was no difference between fruiting and nonfruiting limbs without 6-BA. A similar observation was made by Kender and Carpenter (53). When

fruit were present, 6-BA was ineffective in stimulating lateral vegetative bud emergence.

Both nonfruiting and fruiting limbs had a higher number of viable 'king' flowers when treated with 6-BA (Table 5). The lateral flowers in the cluster did not appear to be affected but this is not very surprising considering the terminal flower will open first making them more susceptible to cold damage. It is assumed flower buds were probably at the tight cluster stage at the time of the cold weather in April since full bloom was not until May 16th. Flower buds at the tight cluster to the full bloom stage may be killed at -2.8 C (27 F), especially when preceeded by warmer weather (77). Thus, death of the 'king' flowers and their ultimate abscission is attributed to the three days in April when the temperature went below freezing. Nonfruiting limbs without 6-BA application also had a higher number of viable 'king' flowers than nontreated fruiting limbs. Fruit will decrease cold resistance (18,104) and this was confirmed here. However, there was no difference between the two after 6-BA treatment and thus there was an increase in the number of viable 'king' flowers on fruiting limbs that was of larger magnitude than on nonfruiting limbs. This is somewhat contrary to many of the variables measured in this investigation, i.e. bloom (Table 4) and flower cluster number (Table 5) in which fruit seemed to partially inhibit the effect of 6-BA. Perhaps this is related to the fact that GA4+7 applications had no effect on viable 'king' flower number (Table 7) and it is GA4+7 which is generally associated with the

inhibitory effects of the fruit.

The beneficial effect of 6-BA in preventing cold damage is undoubtedly indicated. 6-BA was applied many months before and 6-BA metabolism is generally complete within 2 weeks. The increase in cold resistance on 6-BA treated limbs was probably a result of changes in treated spurs during the time of spray application that affected cold resistance to the buds the following spring. Proebsting (77) found spring flower development was an ongoing nonstatic process and at the earlier stages of development (i.e. tight cluster) there are wider temperature differences in determining bud death than at the full bloom stage when there is little temperature variability. It was assumed both treated and nontreated flower buds were at the tight cluster stage of development because bloom did not appear to be delayed on treated buds. Thus, within the tight cluster stage on both treated and nontreated buds there may have been differences in the physiological and/or morphological condition of the spur that determined whether the cold temperatures would result in damage to the 'king' flower. Fruit will decrease cold resistance which is thought to be a result of a reduction in carbohydrate reserves (104). Carbohydrates are important in promoting cold hardiness (106). Earlier it was suggested that fruit alter carbohydrate metabolism in the spur and that 6-BA may help to counteract this effect. Fruiting limbs treated with 6-BA may then have an increased resistance to cold damage as a result of an increase in carbohydrate levels. Cold resistance on 6-BA treated

nonfruiting limbs may have also been increased in this manner but not to the extent of fruiting limbs. Changes in carbohydrate levels from 6-BA applications may not be totally responsible for the increase in cold resistance. Bud vigor was increased on treated limbs as illustrated by 6-BA's effect on flower cluster development (Table 5). Stronger flower buds may have lowered the bud's susceptibility to cold damage. Terminal ('king') flower development may have been delayed somewhat as a result of the increase in lateral flower development making the 'king' flower less susceptible to cold damage.

Differences in treatment effects on bloom in 1981 with GA4+7 and 6-BA and the heavy crop in 1980 appeared to influence fruit set in 1981 more than any direct carryover of spray application. Fruit set results were erratic due to spray treatment and merely reflect bloom differences. In experiment 2 with 6-BA applications, bloom in 1981 was heavier than the other experiments making a few general comparisons about fruit set possible (Table 4). In 1981, fruit set appeared to correspond with some of the observed effects on flower cluster number and percent viable 'king' flowers (Table 5). A lower cluster number and the absence of a 'king' flower would lower the fruit set. Thus, 6-BA most likely influences fruit set in the carryover year indirectly by increasing flower quality.

Effect of 6-BA, GA4+7, and Daminozide on Fruiting

The effects of 6-BA, GA4+7, and daminozide on russeting were consistent with previous reports (74,91). 6-BA increased russeting, GA4+7 decreased it, and daminozide had no effect (Tables 8,11,13). It has not been previously reported however, that combination sprays of 6-BA and GA4+7 counteract the individual effects of one another on russeting. Daminozide has been found to increase russeting but only when two sprays were applied at 2000 ppm each (22,74). The effects of 6-BA and GA4+7 were the same regardless of whether multiple applications started at FB +4 or FB +11 days. Unpublished results of Edgerton and of Taylor (92) have shown using GA4+7 sprays that the critical time period to influence the severity of russeting is at or shortly after bloom.

Increases in fruit length with growth regulator sprays are well known particularly on 'Delicious' (36,60,89,99). Fruit length was increased with GA4+7 and GA4+7 plus 6-BA applications starting at FB +11 days (Table 9) and with GA4+7 or 6-BA when applications began at FB +4 days (Tables 11,14). 6-BA appeared to result in larger increases in length when applications began at FB +4 days. Martin et al (72) have suggested that although cytokinins may be a more powerful elongating agent at or shortly after bloom the effect of gibberellins on fruit length extends beyond bloom and the time period when cytokinins are effective. This effect would seem to be confirmed here since GA4+7 increased fruit length when applications

started at both dates, whereas, 6-BA increased fruit length only when appplications began at FB +4 days. This may have been a factor when 6-BA and GA4+7 were combined because increases in length were no greater than when GA4+7 alone was applied (Table 9). The superiority of combining GA4+7 and 6-BA is well known (89,103) and is used commercially (Promalin) between full bloom and petal fall. However, it has not been previously reported that 6-BA plus GA4+7 will decrease fruit diameter (Table 9) which resulted in an increase in the L/D ratio over GA4+7 treated fruit.

6-BA increased fruit weight when applications started at either FB +4 or FB +11 days (Tables 8,11). There was a corresponding increase in both fruit length and diameter when applications started at FB +4 days but fruit length was increased more than fruit diameter as indicated by the increase in the L/D ratio (Table 11). When applications started at FB +11 days (Table 9) neither fruit length nor diameter were increased when fruit weight was increased (Table 8). Letham (58) reported increases in fruit weight on 'Jonathan' when there no effect on the L/D ratio and attributed it to an increase in cell density in the cortex area of the fruit. He also found on 'Splendour' increases in weight that were accompanied by increases in fruit length which he found was a result of continued growth of the calyx area which did not occur on 'Jonathan'. It has not however been previously reported that 6-BA will increase fruit diameter (Table 11) and it is unclear why this occurred other than perhaps 'Golden Delicious' is more responsive. Martin et al (72) and

Stembridge and Morrell (89) have reported 6-BA was more effective at increasing the L/D ratio, attributed to an increase in fruit length, at earlier application dates. It may be suggested at least on 'Golden Delicious' that the early application (at FB +4 days) was responsible for the increases in fruit length and diameter. Fruit weight increases however, cannot be attributed totally as an indirect effect of increases in either fruit length or diameter or both since there was no effect on fruit length or diameter when applications started at FB +11 days. This suggests the possibility of a direct effect on fruit weight by 6-BA.

Unrath (99) has reported that the response to 6-BA plus GA4+7 on fruit weight reached a maximum at 50% petal fall and decreased from that time onward. Looney (60) however, has reported a maximum increase in fruit weight on 'Spartan' at petal fall +2 weeks. GA4+7 plus 6-BA did not increase fruit weight on 'Golden Delicious' (Table 8). The response to 6-BA plus GA4+7 treatments on fruit weight seems to follow the results of Unrath on 'Delicious'. However, GA4+7 alone increased fruit weight when applications began at FB +11 days (Table (8) but not when applications began at FB +4 days in 1980 (Table 14). The response to GA4+7 alone then seems to follow the results of Looney on 'Spartan'. 6-BA increased fruit weight at both application dates (Tables 8,11) and although the two dates cannot be compared statistically the increase in fruit weight with 6-BA at FB +4 days appears larger than the increase at FB +11 days. The response to 6-BA on 'Golden Delicious' then would appear to follow the results of

Unrath. 6-BA's effect on fruit weight reached a maximum shortly after full bloom and then decreased, while the effect of GA4+7 on fruit weight would appear to reach a maximum at a later date. This suggests the possibility that when 6-BA and GA4+7 are combined they may be counteracting the effects of one another on fruit weight.

Post bloom applications of daminozide may reduce fruit size (5,22). Fisher and Looney (22) reported however that on 'Golden Delicious' post bloom applications of 2000 ppm of daminozide at FB +10 to 18 days did not influence fruit weight. This effect is confirmed here (Table 8). Batjer et al (5) reported that reductions in fruit size were not apparent until FB +50 days and then continued to decline. GA4+7 or plus 6-BA did not increase fruit weight when combined with daminozide. 6-BA plus daminozide increased fruit weight over daminozide treated fruit but this was accompanied by some fruit thinning thus the increase in fruit weight may be a result of a reduction in crop load. Both GA4+7 or 6-BA alone or in combination with each other were able to overcome the reductions in fruit length by daminozide but only 6-BA increased fruit diameter when combined with daminozide. 6-BA then appears to be able to overcome the reductions in both fruit length and diameter from post bloom applications of daminozide. In general, there appears to be a close interrelationship between fruit weight, length, and diameter that is far from being understood. Growth regulator sprays may influence all three variables (weight,length, and diameter) independently or as a consequence of an effect on one or the other.

Daminozide and 6-BA alone or in combination had no effect on seed number (Tables 10,12). GA4+7 alone decreased seed number and when combined with 6-BA seed number was decreased even more (Tables 10,15). Edgerton (21) has also reported a decrease in seed number with GA4+7 on 'Golden Delicious'. Greene et al (36) reported a linear decrease in seed number with increasing concentrations of both 6-BA and GA4+7. However, the synergistic decrease in seed number when 6-BA and GA4+7 are combined has not been shown before. Seed number is often lower with growth regulator treatments that increase fruit set because the fruit that normally would have dropped with low seed numbers are retained (111,112). Only two of the treatments affected fruit set. 6-BA plus daminozide decreased set and GA4+7 plus daminozide increased fruit set (Table 1). This appeared to be related more to a daminozide interaction with either 6-BA or GA4+7 and fruit set and not to seed number. Thus, it would appear that on treatments that decreased seed number it was independent of a fruit set effect suggesting GA4+7 alone and combined with 6-BA maybe capable on influencing seed abortion.

BIBLIOGRAPHY

1. Abbott, D.L. 1960. The bourse shoot as a factor in the growth of apple fruits. Ann. Appl. Biol. 48:434-438.

2. Abbott, D.L. 1970. The role of budscales in the morphogenesis and dormancy of the apple fruit bud, pp. 65-80. In L.C. Luckwill and C.V. Cutting (Eds.) Physiology of tree crops. Academic Press. New York.

3. Abbott, D.L. 1977. Fruit bud formation in Cox's Orange Pippin. Rep. Long Ashton Res. Station for 1976. pp. 167-176.

4. Abeles, F.B. 1973. Ethylene in plant biology. Academic Press, New York.

5. Batjer, L.P., M.W. Williams, and G.C. Martin. 1964. Effects of N-dimethylamino succinamic acid (B-Nine) on vegetative and fruit characteristics of apples, pears, and sweet cherries. Proc. Amer. Soc. Hort. Sci. 85:11-16.

6. Bernier, G. 1971. Structural and metabolic changes in the shoot apex in transition to flowering. Can. J. Bot. 49:803-819.

7. Bernier, G., J. Kinet, and R.M. Sachs. 1981. The physiology of flowering. Vol 2. CRC Press, Boca Raton, Florida.

8. Bradley, M.V. and J.C. Crane. 1960. Gibberellin induced inhibition of bud development in some species of Prunus. Science 131:825-26.

9. Buban, T. and I. Simon. 1978. Cytochemical investigations in apices of apple buds with special reference to flower initiation. Acta. Hort. 80:193-198.

10. Buban, T. and M. Faust. 1982. Flower bud induction in apple trees: Internal control and differentiation. Hort Reviews 4:174-203.

11. Burke, M.J., L.V. Gusta, H.A. Quamme, C.J. Weiser, and P.H. Li. 1978. Freezing and injury in woody plants. Ann. Rev. Plant Phys. 27:507-528.

12. Chan, B. and J. Cain. 1967. The effect of seed formation on subsequent flowering in apple. Proc. Amer. Soc. Hort. Sci. 91:63-68.

13. Chvojka, L., K. Veres, and J. Kozel. 1961. Effect of kinins on the growth of apple tree buds and on incorporation of radioactive phosphate. Biol. Plant. 3:140-147.

14. Davis, L.D. 1957. Flowering and alternate bearing. Proc. Amer. Soc. Hort. Sci. 70:545-56.

15. Dennis, F.G.Jr. and L.J. Edgerton. 1966. Effects of gibberellins and ringing upon apple fruit development and flower bud formation. Proc. Amer. Soc. Hort. Sci. 88:14-24.

16. Dennis, F.G.Jr. and J.P. Nitsch. 1966. Identification of gibberellins A4 and A7 in immature apple seeds. Nature 211:781-82.

17. Dennis, F.G.Jr. 1976. Trials of ethephon and other growth regulators for delaying bloom in tree fruits. J. Amer. Soc. Hort. Sci. 101:241-45.

18. Edgerton, L.J. and M.B. Hoffman. 1952. The effect of thinning peaches with bloom and post bloom sprays on the cold hardiness of the fruit buds. Proc. Amer. Soc. Hort. Sci. 60:155-159.

19. Edgerton, L.J. and M.B. Hoffman. 1964. Some physiological responses of apple to N-dimethylamino succinamic acid and other growth regulators. Proc. Amer. Soc. Hort. Sci. 86:28-36.

20. Edgerton, L.J. 1966. Some effects of gibberellin and growth retardants on bud development and cold hardiness of peach. Proc. Amer. Soc. Hort. Sci. 88:197-203

21. Edgerton, L.J. 1981. Some effects of aminoethoxvinylglycine, 6-benzylaminopurine and gibberellins on fruit set and vegetative growth of apple. Acta Hort. 120:125-30.

22. Fisher, D.V. and N.E. Looney. 1969. Growth, fruiting and storage response of five cultivars of bearing apple trees to N-dimethylamino succinamic acid (Alar). Proc. Amer. Soc. Hort. Sci. 90:9-19.

23. Forshey, C.G. 1975. Vegetative growth control in apple trees. Proc. NY State Hort. Soc. 120:152-58.

24. Friedrick, A., L. Chvojka, R. Bulgakov, and J. Kolin. 1970. Transport, localization, and physiological effect of 6-benzyladenine 8 C in apple shoots. Biol. Plant 11:342-347.

25. Friedrick, A., L. Hejmova, and L. Chvojka. 1972. Substances with cytokinin activity extracted from growing apices of apple tree shoots. Biol. Plant 14:164-166.

26. Fulford, R.M. 1965. The morphogenesis of apple buds. I. The activity of the apical meristem. Ann. Bot. 29:167-180.

27. Fulford, R.M. 1966. The morphogenesis of apple buds. II. The development of the bud. Ann. Bot. 30:25-38.

28. Fulford, R.M. 1966. The morphogenesis of apple buds. III. The inception of flowers. Ann. Bot. 30:207-219.

29. Fulford, R. M. 1966. The morphogenesis of apple buds. IV. The effect of fruit. Ann. Bot. 30:597-606.

30. Fulford, R.M. 1973. Effect of gibberellin sprays. Report for East Malling Res. Sta. for 1972. pp.93.

31. Fulford, R.M. 1980. Flower initiation and development. Report for East Malling Res. Sta. for 1979. pp.181.

32. Goff, E.F. 1899,1900,1901. Investigations of flower buds. Rep. Wis. agric. Exp. Sta., No. 16,17, and 18..

33. Gourley, J.H. 1915. Studies in fruit bud formation. Tech. Bull. N.H. agric. Exp. Sta. No. 9.

34. Greene, D.W. 1980. Effect of silver nitrate, aminoethoxyvinylglycine, and gibberellins A4+7 plus 6-benzylaminopurine on fruit set and development of 'Delicious' apple. J. Amer. Soc. Hort. Sci. 105:717-20.

35. Greene, D.W. 1981. Growth regulator application and cultural techniques to promote early fruiting of apples. In Tree Fruit Growth Regulators and Chemical Thinning-Short Course Proceedings. Eds. R.B. Tukey and M.W. Williams. Washington State University.

36. Greene, D.W., W.J. Lord, and W.J. Bramlage. 1982. Effects of gibberellins A4+7 and 6-benzylaminopurine on fruit set, fruit characteristics, seed content, and storage quality of 'McIntosh' apples. HortScience 17:653-54.

37. Grochowska, M.J. 1968. The influence of growth regulators inserted into apple fruitlets on flower bud initiation. Bull. Acad. pol. Sci., Sci. biol. 16:581-84.

38. Grochowska, M.J. 1973. Comparative studies on physiological and morphological features of bearing and nonbearing spurs of the apple tree. I. Changes in starch content during growth. J. Hort. Sci. 48:347-56.

39. Grochowska, M.J. 1973. Comparative studies on physiological and morphological features of bearing and nonbearing spurs of the apple tree. II. The effect of fruiting and growth regulator sprays on the respiration rate of leaves. Physiol. Plant. 29:425-29.

40. Grochowska, M.J. and A. Karaszewska. 1976. The production of growth promoting hormones and their active diffusion from immature, developing seeds of four apple cultivars. Fruit Science Reports. 3:6-16.

41. Grochowska, M.J. and A. Karaszewska. 1978. A possible role of hormones in growth and development of apple trees and a suggestion on how to modify their action. Acta Hort. 80:457-64.

42. Guttridge, C.G. 1962. Inhibition of fruit bud formation in apple with gibberellic acid. Nature 196:1006.

43. Harley, C.P., J.R. Magness, M.P. Masure, L.A. Fletcher, and E.S. Degman. 1942. Investigations on the cause and control of biennial bearing of apple trees. U.S. Dept. Agri. Tech. Bul. 792.

44. Harley, C.P., H.H. Moon, and L.O. Regeimbal. 1958. Evidence that post- bloom apple thinning sprays of napthalenacetic acid increase blossom bud formation. Proc. Amer. Soc. Hort. Sci. 72:52-56.

45. Hall, J.Jr. and L.N. Lewis. 1959. Response of one-year-old cherry and mature cherry, peach, and apple trees to gibberellin. Proc. Amer. Soc. Hort. Sci. 74:93-100.

46. Hoad, G.V. and S.P. Monselise. 1976. Effects of succinic acid 2,2-dimethylhydrazide (SADH) on the gibberellin and abscisic acid levels in stem tips of M26 apple rootstocks. Scientia Hort. 4:41-47.

47. Hoad, G.V., B.R. Loveys, and K.D. Skene. 1977. The effect of fruit removal on cytokinins and gibberellin-like substances in grape leaves. Planta 136:25-30.

48. Hoad, G.V. 1978. The role of seed derived hormones in the control of flowering in apple. Acta Hort. 80:93-103.

49. Hoad, G.V. 1980. Growth regulators, endogenous hormones and flower initiation in apple. Rep. Long Ashton Res. Station for 1979. pp.199-206.

50. Hooker, H.D.Jr. 1920. Seasonal changes in the chemical composition of apple spurs. Mo. Agr. Expt. Sta. Res. Bul., 40.

51. Jindal, K.K., A. Skytt Anderson, and S. Dalbro. 1975. Ethylene evolution stimulated by succinic-2,2 dimethylhydrazide in apple shoots. Physiol. Plant. 34:26-29.

52. Jindal, K.K. and S. Dalbro. 1977. Effect of 2,2-dimethylhydrazide on endogenous auxin levels in apple shoots. Physiol. Plant. 36:119-22.

53. Kender, W.J. and S. Carpenter. 1972. Stimulation of lateral bud growth of apple trees by 6-benzylaminopurine. J. Amer. Soc. Hort. Sci. 97:377-80.

54. Kraus, E.J. and H.R. Kraybill. 1918. Vegetation and reproduction with special reference to the tomato. Oreg. Agr. Exp. Stat. Bul. 149.

55. Kuo, C.G. and R.P. Pharis. 1975. Effects of AMO-1618 and B-995 on growth and endogenous gibberellin content of Cupressus arizonica seedlings. Physiol. Plant. 34:788-92.

56. Lazariceva, S. 1967. Leaf development in biennially bearing apple varieties. Sadovodstvo 6:32. (Hort. Abstr. 38:398).

57. Letham, D.S. 1969. Regulators of cell division in plant tissues. VI. The effects of zeatin and other stimulants of cell division on apple fruit development. N.Z. Jl. agric. Res. 12:1-20.

58. Letham, D.S. and M.W. Williams. 1969. Regulators of cell division in plant tissues. VIII. The cytokinins of the apple fruit. Physiol. Plant. 22:925-36.

59. Lipecki, J. and E. Slaska. 1976. Effect of Gibrescol/GA3/ on the levels of gibberellin-like substances in apple spurs. Fruit Science Reports. 3:35-38.

60. Looney, N.E. 1979. Some effects of gibberellins A4+7 plus 6-benzyladenine on fruit weight, shape, quality, Ca content, and storage behavior of 'Spartan' apple. J. Amer. Soc. Hort. Sci. 104:389-91.

61. Low, V.H.K. 1975. Role of gibberellins in root and shoot growth. In Gibberellins and Plant Growth. Ed. H.N.Krishnamoorthy. John Wiley and Sons, New York. pp.101-14.

62. Luckwill, L.C. and P. Whyte. 1968. Hormones in the xylem sap of apple trees. In Plant Growth Regulators Monograph 31. Society of Chemical Industry. pp.87-101.

63. Luckwill, L.C. 1969. The control of growth and fruitfulness of apple trees. In Physiology of Tree Crops. Eds. L.C. Luckwill and C.V. Cutting. Academic Press, New York. pp.237-54.

64. Luckwill, L.C., P. Weaver, and J. MacMillan. 1969. Gibberellins and other plant growth hormones in apple seeds. J. Hort. Sci. 44:413-21.

65. Luckwill, L.C. 1974. A new look at the process of fruit bud formation in apple. Proc. 19th Inter. Hort. Congress (Warsaw) 3:237-45.

66. Luckwill, L.C. and J.M. Silva. 1979. The effects of daminozide and gibberellic acid on flower initiation, growth, and fruiting of apple cv. Golden Delicious. J. Hort. Sci. 54:217-223.

67. Mack, W.B. 1924. Habits of growth and bearing of apple varieties as related to biennial bearing. Proc. Amer. Soc. Hort. Sci. 21:296-300.

68. Magness, J.R., L.A. Fletcher, and W.W. Aldrich. 1934. Time during which fruit bud formation in apples may be influenced in the Shenandoah- Cumberland fruit districts. Proc. Amer. Soc. Hort. Sci. 30:313-18.

69. Marcelle, R. and C. Sironval. 1963. Effect of gibberellic acid on flowering of apple trees. Nature 197:405.

70. Marino, F. and D.W. Greene. 1981. Involvement of gibberellins in the biennial bearing of 'Early McIntosh' apples. J. Amer. Soc. Hort. Sci. 106:593-96.

71. Marsh, H.V., F.W. Southwick, and W.D. Weeks. 1962. The influence of chemical thinners on fruit set and size, seed development, and preharvest drop of apples. Proc. Amer. Soc. Hort. Sci. 75:5-21.

72. Martin, G.C., D.S. Brown, and M.N. Nelson. 1970. Apple shape changing possible with cytokinin and gibberellin sprays. Calif. Agric. 24(4):14.

73. Martin, G.C., R. Horgan, and C. Nishijima. 1982. Changes in hormone content of pear receptacles from anthesis to shortly after fertilization as affected by pollination or GA3 treatment. J. Amer. Soc. Hort. Sci. 107:479-82.

74. McDonnell, P.F. and L.J. Edgerton. 1970. Some effects of CCC and Alar on fruit set and fruit quality of apple. HortScience 5:89-91.

75. Monselise, S.P. 1973. Recent advances in the understanding of flower formation in fruit trees and its hormonal control. Acta Hort. 34:157-66.

76. Phillips, I.D.J. 1975. Apical dominance. Ann. Rev. Plant Physiol. 26:341-67.

77. Proebsting, E.L. and H.H. Mills. 1978. Low temperature resistance of developing flower buds of six deciduous fruit species. J. Amer. Soc. Hort. Sci. 103:192-98.

78. Prokopy, R.J., G.L. Hubbell, W.M. Coli, and W.J. Lord. 1980. Excessive apple bud abscission in 1980:Was it caused by tarnished plant bug feeding or cold temperatures. Fruit Notes 45:13-14.

79. Raese, T. 1977. Induction of cold hardiness in apple tree shoots with ethephon, NAA, and growth retardants. J. Amer. Soc. Hort. Sci. 102:789-92.

80. Ramirez, H.R. and G.V. Hoad. 1978. Effect of succinic acid 2,2-dimethyl hydrazide (SADH) and hormones on flower initiation in apple. Monograph 2-1978. British Plant Growth Regulator Group. pp.37-47.

81. Ramirez, H.R. 1979. Effects of growth substances on some physiological processes in apple in relation to flower intiation. pp.181. PhD. thesis, University of Bristol. England.

82. Roberts, R.H. 1920. Off year bearing and apple spur growth. Res. Bull. Wisc. agric. Exp. Sta., 317.

83. Sachs, R.M. 1977. Nutrient diversion: An hypothesis to explain the chemical control of flowering. HortScience 12:220-22.

84. Skene, K.G.M. 1968. Increases in the levels of cytokinins in bleeding sap of Vitis vinifera, L. after CCC treatment. Science 159:1477-78.

85. Singh, L.B. 1948. Studies in biennial bearing. II. A review of the literature. III. Growth studies in the 'on' and 'off' years of apple trees. J. Hort. Sci. 24:45-65, 123-48.

86. Southwick, F.W., W.D. Weeks., and W.J. Lord. 1967. The influence of some growth regulators and techniques on the flowering, abscission, growth, yield, and physiological disorders of apples. Ann. Rep. Mass. Fruit Grower's Assn. 73:59-69.

87. Srinivasan, C. and M.G. Mullins. 1978. Control of flowering in the grapevine (Vitis vinifera L.): Formation of infloresences in vitro by isolated tendrils. Plant Phsiol. 61:127-30.

88. Steel, R.G. and J.H. Torrie. 1960. Priniciples and procedures of statistics. McGraw Hill, New York. pp.232-41.

89. Stembridge, G.E. and G. Morrell. 1972. Effect of gibberellins and 6-BA on the shape and fruit set of 'Delicious' apples. J. Amer. Soc. Hort. Sci. 97:464-67.

90. Stembridge, G.E. 1973. Effect of growth regulators on the size and shape of fruits. Acta Hort. 34:435-40.

91. Taylor, B.K. 1975. Reduction of apple skin russeting by gibberellin A4+7. J. Hort. Sci. 50:169-72.

92. Taylor, B.K. 1978. Effects of gibberellin sprays on fruit russet and tree performance of Golden Delicious apple. J. Hort. Sci. 53:167-69.

93. Trewavas, A.J. 1982. Growth substance sensitivity: The limiting factor in plant development. Physiol. Plant. 55:60-72.

94. Tromp, J. 1972. Effects of growth regulating substances and tree orientation on growth and flower bud formation in apples. J. Hort. Sci. 47:525-533.

95. Tromp, J. 1973. The interaction of growth regulators and tree orientation on fruit bud formation. Acta Hort. 34:185-88.

96. Tromp, J. and S.J. Wertheim. 1980. Physiological aspects of crop productivity. Proc. 15th Colloq. Int. Potash Institute, Bern. pp. 137-50.

97. Tucker, L.R. and G.F. Potter. 1929. Characteristics of growth and fruiting in the Baldwin apple. Proc. Amer. Soc. Hort. Sci. 25:237-43.

98. Tumanov, I.I. and E.Z. Gareev. 1951. The effect of fruiting organs on the mother plant. Trudy Inst. Fiziol. Rast. Timirjazeva 7:22-108. (Hort Abstracts)

99. Unrath, C.R. 1974. The commercial implications of gibberellin A4+7 plus benzyladenine for improving shape and yield of 'Delicious' apples. J. Amer. Soc. Hort. Sci. 94:381-84.

100. van Staden, J. and J. Butten. 1978. The cytokinin content of aseptically cultured pea plants. Z. Pflanzenphysiol. 87:129-38.

101. Varga, A. 1969. Effects of growth regulators on fruit set and June drop of pears and apples. Neth. J. Agric. Sci. 17:229-33.

102. Walsh, C.S., H.J. Swartz, L.J. Edgerton. 1979. Ethylene evolution in apple following post bloom thinning sprays. HortScience 14:704-6.

103. Walsh, C.S. 1980. Studies of ethylene evolution in apple. HortScience 5:60.

104. Way, R.D. 1954. The effect of some cultural practices and of size of crop on the subsequent winter hardiness of apple trees. Proc. Amer. Soc. Hort. Sci. 63:163-66.

105. Weiner, B.J. 1971. Statistical Principles of Experimental Design. McGraw Hill, New York. pp.397-402.

106. Weiser, C.J. 1970. Cold resistance and injury in woody plants. Science 169:1269-78.

107. Wilde, M.H. and L.J. Edgerton. 1969. Some effects of a growth retardant on shoot meristems of apple. J. Amer. Soc. Hort. Sci. 94:118-22.

108. Williams, M.W. and E.A. Stahly. 1968. Effects of cytokinins on apple shoot development from axillary buds. HortScience 3:68-69.

109. Williams, M.W. and E.A. Stahly. 1969. Effect of cytokinins and gibberellins on shape of 'Delicious' apple fruits. J. Amer. Soc. Hort. Sci. 94:17-19.

110. Williams, M.W. 1973. Chemical control of vegetative growth and flowering of apple trees. Acta Hort. 24:167-74.

111. Williams, M.W. 1979. Chemical thinning of apples. Hort Reviews 1:270-300.

112. Williams, M.W. 1980. Fruit thinning of apples and pears with chemicals. Agricultural Information Bulletin, 289.

APPENDIX

Experiment 4. Effect of Selected Cytokinins on Flowering

Sixteen trees were paired into 8 groups and seven limbs were selected from each group and randomly assigned to one of the following seven treatments: 1) zeatin, 2) zeatin riboside, 3) 6-benzylaminopurine, 4) kinetin, 5) isopentyladenine, 6) 2-isopentyladenine, and 7) distilled water or the check. Treatments were applied with a microsyringe in droplets to a cut petiole. Treatments 1 through 6 were applied in 10 uL quantities from a .02 M stock solution. 10 uL of distilled water was applied for the check. On each limb 5 shoots, 20 nonfruiting spurs, and 20 fruiting spurs were selected. On each shoot, treatments were injected into the axils of 5 midleaves and the 5 most terminal buds. Nonfruiting spurs were defoliated to two leaves and treatments applied via cut petiole. On fruiting spurs, a leaf was cut and the treatments applied to the tip of the cut petiole. On shoots treatments were applied at 6 and 8 weeks after full bloom. Nonfruiting spurs wwere defoliated on June 2 to June 4, 1980. Treatments were applied to both nonfruiting and fruiting spurs at 3 and 7 weeks after fuull bloom.

Return bloom was evaluated in 1981 following treatment in 1980. During the summer of 1980, many of the treated buds broke and began to develop particularly on the 6-BA treatments and on nonfruiting spurs. However, in 1981 there was no return bloom on any of the treatments. The results did not appear to be conclusive and thus were not included in the main text.