M. RAHEMI

PH. D.

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M. RAHEMI

This is to certify that the

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Majid Rahemi

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Frank G. Dennis Jr.
Major professor

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ROLE OF ETHYLENE AND THE EFFECT OF SUPPLEMENTAL HAND POLLINATION IN APPLE (*MALUS DOMESTICA* BORKH.) FRUIT SET

By

Majid Rahemi

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ABSTRACT

ROLE OF ETHYLENE AND THE EFFECT OF SUPPLEMENTAL HAND POLLINATION IN APPLE (MALUS DOMESTICA BORKH.) FRUIT SET

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To determine the role of ethylene in apple fruit set, aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, silver thiosulfate (STS), an inhibitor of ethylene action, and (2-chloroethyl) phosphonic acid (ethephon), an ethylene generating compound, were applied in 1980 and 1981 to branch units of 'McIntosh', 'Delicious', and 'Golden Delicious' apple trees at full bloom and/or at 18 to 21 days after full bloom. Additional branches were scored with a knife.

When applied at full bloom AVG (200 ppm) significantly increased set in all cultivars, but effects of 100 ppm were generally non-significant. Although both concentrations reduced ethylene evolution from flowers excised 1 to 10 days after treatment, the effects were small and non-significant. Ethephon (40 to 100 ppm) did not affect fruit set significantly, yet markedly increased ethylene

production. Fruit set was much better correlated with ethylene evolution in 'Delicious'than in 'McIntosh' or 'Golden Delicious', but r values were non-significant. Therefore the effects of AVG on fruit set appear to be independent of its effects on ethylene synthesis.

Application of AVG (200 ppm) prior to "June" drop had no significant effect on ethylene evolution in any of the three cultivars. The chemical significantly reduced fruit retention in 'McIntosh' and increased it in 'Delicious' in 1980, but had no significant effects in 1981. Neither STS nor scoring had consistent effects on either set or ethylene evolution. Ethephon (200 ppm) significantly increased both fruit drop and ethylene evolution in all three cultivars, but 100 ppm was effective only in 'McIntosh' and 'Golden Delicious'. Ethylene evolution prior to and during "June" drop was measured in two populations of fruits selected on the basis of diameter. Small fruits with a higher abscission potential generally produced more ethylene per unit weight than large fruits sampled at the same time. However, when the rate of ethylene production of non-treated fruits was plotted against fruit weight, rather than against date of sampling, abscission potential appeared to be independent of ethylene production. These data suggest that differences in the rate of ethylene evolution were due to the differences in size, rather than to differences in abscission potential, and that ethylene is not the primary factor responsible for "June" drop.

Aqueous sprays of AVG were applied at full bloom to flowers on bagged limbs of 'McIntosh' and 'Delicious' to determine its effect on the effective pollination period. AVG-treated and control flowers were hand-pollinated with 'Empire' pollen at 1 to 3 day intervals beginning at anthesis. AVG (200 ppm) increased fruit set in 'Delicious' but not in 'McIntosh'. Fruit set decreased as the time of pollination was delayed and response of AVG-treated flowers paralleled that of control flowers. The data obtained in this study indicate that AVG has little or no effect on the effective pollination period.

To test the hypothesis that "basal gaps" between the stamens of 'Delicious' flowers limit fruit set by permitting bees to obtain nectar without transferring pollen to the stigmata, open-pollinated flowers of 'Delicious' and 'McIntosh' were hand-pollinated at anthesis. Supplemental hand pollination increased initial and final fruit set in 'Delicious' but not in 'McIntosh', supporting the hypothesis. However, final set of open pollinated flowers was no greater in 'McIntosh' than in 'Delicious'. The results are therefore inconclusive. Staining with aniline blue made pollen tubes visible in the entire length of 'McIntosh' styles, but only in the upper half of 'Delicious' styles. Many pollen tubes in open- and open-plus hand-pollinated flowers reached the base of 'McIntosh' styles within 4-6 days, but very few reached the base in self-pollinated (bagged) flowers and most terminated in swollen tips and highly caloused plugs. Such flowers set almost no fruits.

Dedicated to

The Martyrs of the Islamic Revolution of Iran

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The journal-article format was adopted for this dissertation in accordance with departmental and university requirements. Four sections were prepared and styled for publication in the Journal of the American Society for Horticultural Science.

INTRODUCTION

Although 4,000 to 5,000 cultivars of apple had been described by 1938 (Hedrick 1938) only two dozen cultivars accounted for 95% of the total commercial crop in the United States in 1969 (Henderson et al. 1969). The leading cultivar in the United States, 'Delicious', represented 30% of the total U.S. production in 1969 and 35% in 1975 (USDA, 1977). 'Golden Delicious' ranked second and accounted for 13% in 1975. Other leading varieties were 'McIntosh', 10%; 'Rome Beauty', 8%; 'Jonathan', 6%; and 'York Imperial', 5%.

'Delicious' is now the world's most popular variety. Its high color and characteristic shape make it a favorite of both grower and consumer. According to Maas (1970) no variety of apple of American origin was ever accepted more readily by the American public.

Despite being the leading apple variety and having a higher market demand, 'Delicious' is recognized as a light bearer. In 1928 Howlett stated .... "that the 'Delicious' apple under certain growth conditions tends to be a relatively light yielding variety is gradually becoming recognized. In Ohio 'Delicious' has shown a tendency to set light even in mixed plantings". Young Delicious trees

often bear light crops for several years after coming into production. Greene and Lord (1978) stated that lack of flower bud initiation and/or fruit set often limits the productivity of young 'Delicious' apple trees. The light yields are due at least in part to light fruit setting rather than to irregular and light fruit bud formation (Howlett, 1928).

'Delicious' performs better in Washington State, presumably because of higher solar radiation (Way 1973). In the eastern states production of 'Delicious' remains a continuing challenge because of erratic and low yields per acre. Currently research is being directed toward methods for increasing yields of 'Red Delicious' in eastern regions.

The purpose of this study was to determine the role of ethylene and the effect of supplemental hand pollination in controlling fruit set and development of apples under orchard conditions.

REVIEW OF LITERATURE

I. Delicious Apple Production in the United States

The 'Delicious' apple is one of the most desirable of all the varieties grown commercially in the United States (Forshey, 1953). Of 17 leading varieties,production of only 'Delicious', 'McIntosh', 'Golden Delicious', and 'Cortland' has increased appreciably in the U.S. since 1942 (Childers, 1969), with 'Delicious' and 'Golden Delicious' increasing spectacularly. In Washington State 'Delicious' yields heavy crops. Tukey (1978) stated that good management, skill and hard work are important elements to bring trees into production. Since about 1950 'Delicious' and other varieties have been yielding better under Eastern U.S. conditions, apparently due to the use of milder fungicides and better cultural practices and strains (Childers, 1969; Way, 1973). Over 150 red strains of 'Delicious' have been named but many have not been fully evaluated for yield and/or fruit quality. 'Starking' and 'Richared' are two strains which are widely planted (Childers 1969). Dennis (1979) summarized published yield differences of several strains of 'Delicious' in the United States, Italy and Poland and concluded that "strain has a marked influence

on yield, although the spur strains appear to be less variable than non-spur strains".

U.S. 'Delicious' production more than doubled in the last twenty years, increasing from an average of 500 million (26 million bushels) in the early 1950's to 1090.1 million Kg (58 million bushels) in 1974-1977 (Ricks and Pierson 1978). Planting of 'Delicious' increased in most regions during the last two decades, particularly in Washington State. Washington production increased from an average of approximately 404.06 million Kg (21 million bushels) during the early 1970's to 590.2 Kg in 1977, an increase of 47% within just five years. Washington now produces about 55% of the national 'Delicious' crop (Ricks and Pierson, 1978). Production of 'Delicious' in eastern states has risen only gradually, in part because of continuing erratic and low yield per acre.

II. Factors Affecting Fruit Set of Delicious

A. Environmental Factors

Environmental conditions during bloom and early post bloom affect the performance of pollinating insects as well as the blossoms themselves. Bee activity is reduced by low temperature. Low temperature following pollination may reduce fruit set either by injury to pollen or pistil (Boyd and Latimer 1933). Differences in frost susceptibility

exist among cultivars and 'Delicious' flowers are more susceptible to frost injury than flowers of many other cultivars (Hartman and Howlett, 1954; Roberts, 1946, Meader and Blasberg, 1946, Westwood et al., 1976). Wilson and Williams (1970) and Forshey (1978) suggested that sub-lethal injury may reduce the fruit-setting capacity of flowers which survive a freeze, but no data are available to support this suggestion.

Temperature may have important effects on pollination, pollen tube growth and bee activity. Low temperature following pollination may reduce the set of fruit by slowing down pollen tube growth so that the sperm nuclei do not reach the embryo sac before disintegration commences (Boyd and Latimer 1933). Gardner et al (1949) collected data from 41 'Delicious' orchards across the United States and in Nova Scotia, and concluded that temperature was one of the critical factors controlling fruit set in 'Delicious' with high temperature favoring and low temperature reducing set. On the other hand Roberts (1947) believed that warm nights decreased fruit set in 'Delicious'. Lu and Roberts (1952) hand pollinated flowers on apple trees held in greenhouses at 21 to 24°C or a minimum of 13. Better fruit set occurred in 'Delicious', 'McIntosh' and 'Wealthy' under cool than under warm conditions. They also reported that 'Delicious' blossoms dropped heavily at temperatures above 21°. Lapins and Arndt (1974) reported

that optimum temperature for pollen tube growth in 'Delicious' flowers was between 7.2°-12.8° and that pollen grains failed to germinate below 4.4°. They also reported that pollen tubes could reach the base of the style in 3 days at an average day-night temperature of 12.8° and in 5 days at an average temperature of 7.8. Forshey (1977) reported that apple pollen tube growth practically ceased at 7.2°C.

Cool temperatures reduce bee activity during bloom and may affect fruit set in apples. Lu and Roberts (1952) attributed poor setting of 'Delicious' during cool blossom periods to poor bee activity. Brittain (1933) studied bee activity in Nova Scotia apple orchards and found a rise in activity from 10 to 18°C followed by a gradual decrease to a low level at 30°. Although limited honey bee flight occurs at 15° to 18°, full flight requires temperatures exceeding about 21° (Morse 1975).

Reports on the effects of sunshine and cloudiness on fruit set during bloom are conflicting. Boyd and Latimer (1933) reported that lack of sunshine and cloudy weather were not detrimental to fruit setting in the apple. They obtained a heavy set of fruit when hand pollination was performed during humid, cloudy or rainy weather with mild temperature. They attributed the better results obtained from pollination performed on cloudy days to high humidity. However, Gardner, et al.(1949) associated high fruit set of 'Delicious' with high radiant energy during the week after

full bloom. Subsequently Dennis (1979) analyzed their data and found correlation coefficients were low and non-significant.

Rain has no effect on fruit set unless, of course, it continues throughout bloom and prevents bee flight (Griggs 1958). Boyd and Latimer (1933) found that heavy rain did not wash pollen from the stigmas in sufficient quantity to be detrimental to obtaining a satisfactory set of fruit. They reported that set was as good following a heavy rain as following cloudy weather and high humidity without rainfall.

B. Pollination

Delicious is totally self-unfruitful (Howlett, 1928; Overholser and Overly, 1931; Roberts, 1945) and cross pollination is essential for consistent heavy production. Howlett (1928) concluded that a considerable part of light fruit setting of 'Delicious' is due to inadequate pollination. However, even with adequate cross pollination 'Delicious' was less productive than such heavy setting varieties as 'Jonathan', 'Grimes', 'Baldwin', 'Wealthy' and 'Yellow Transparent' (Howlett 1928). Several factors may contribute to unsatisfactory pollination of 'Delicious'.

1. Flower Structure

Most apple flower clusters, which contain 5-6 flowers, are produced on spurs on 2- to 3-year-old wood, although some are borne laterally on 1-year-old wood. The apple flower produces both nectar and pollen in greater abundance than most other deciduous fruit trees (Smith and Bradt, 1967). Roberts (1945) concluded that one reason for the poor set of 'Delicious' was the relative length of the pistils and stamens; the pistils were so short that bees which collected only pollen did not always touch the stigma. Forshey (1953) measured the length of pistils and stamens in several cultivars, and reported that they were of equal length in 'Delicious', 'Jonathan' and 'Rome Beauty'. He concluded that the structure of blossom is not responsible for poor set of 'Delicious'. However, Roberts (1945) also reported that the structure of 'Delicious' blossoms permits honey bees to remove nectar without pollination of the stigma; only about 20 percent of the bees visiting the flowers crawled over the stigma. Robinson (1980) reported similar "sideworking" of honey bees on 'Delicious' blossoms as a result of "basal gaps" or spaces between stamens. The maximum width of the tongue (glossa) of a honey bee is about 180μ. Robinson measured the percent of basal gaps larger than 180 μ between stamens in several cultivars of apple. He found the width of these gaps to be greater in 7 'Delicious' sports than in 11 other cultivars.

Therefore, nectar collection through basal gaps was more difficult in cultivars such as 'Golden Delicious', 'McIntosh', 'Idared', 'Cortland', 'Jonathan' and 'Rhode Island Greening' than in several 'Delicious' strains or in 'Northern Spy', which also exhibits large basal gaps. He believed that the behavior of honey bees on apple blossoms is determined by the presence or absence of these basal gaps, which reduce the rate of cross-pollination.

2. Pollinizer Cultivar

Investigators have used techniques such as hand pollination and bagging or emasculating blossoms to determine the effectiveness of various commercially important cultivars as pollinizers for 'Delicious'. Overholser and Overly (1931) reported that 'Blackjon', 'King John', 'Red Rome', 'Jonathan' and 'Rome Beauty' were satisfactory pollinizers. All red sports of 'Delicious' tested, with the exception of 'Van Buren', have proven to be incompatible with the parental variety and thus should not be used as pollinizers (Wellington, 1947). All of the triploids such as 'Baldwin', 'Rhode Island Greening', 'Stayman' and 'Winesap' have 51 chromosomes, an uneven number. They therefore produce pollen of low germination and consequently are not reliable pollinators (Overholser and Overly, 1931; Wellington, 1947). The diploid cultivars have 34 chromosomes in each somatic

cell and produce good or at least a fair amount of viable pollen (Wellington,1947). Roberts (1947) made a survey to compare fruit set in 166 blocks of 'Delicious' from Arkansas and Minnesota to Virginia and Nova Scotia and around the Great Lakes. He found a consistent record of good set of 'Delicious' when pollinizers set well. He noted that the best pollinizers, based upon yield of 'Delicious', were 'Rome Beauty' and 'Northern Spy'. 'McIntosh' and 'Winesap' (triploid) were intermediate. 'Winter Banana' and 'Baldwin' (triploid) were relatively poor and 'Rhode Island Greening' (triploid), 'Duchess' and 'Stayman' (triploid sport of 'Winesap') very poor. The value of 'Golden Delicious' as a pollinizer for the 'Delicious' is uncertain. Whitehouse and Auchter (1927) noted that 5.8 to 9.8% of flowers of 'Delicious' hand pollinated with 'Golden Delicious' pollen set fruit whereas open pollinated blossoms set 16.7%. Knowlton (1929), however, reported that 'Golden Delicious' was a good pollinizer of 'Delicious' in West Virginia. Overholser and Overly (1931) found that the pollen of 'Golden Delicious' gave an average set of 11.6% vs. 14.1% for 'Jonathan' pollen when used on 'Delicious' over a 3-year period (1928-31). Tukey (1978) considered 'Winter Banana' to be superior to 'Golden Delicious' as a pollinizer for 'Delicious' in Washington State because it blooms early, overlapping the king flower of 'Delicious'. Hull (1978) stated that 'Jonathan', 'Empire' and 'Idared' have performed

well in Michigan as pollinizer cultivars for 'Delicious'.

In planting solid blocks of commercial apple cultivars, use of top grafts of pollinizers or interplanting small trees of flowering crabapple may correct the cross pollination problem (Hoffman, 1966; Williams, 1972). Artificial pollination techniques may be required to increase the crop in rows far from pollinizers even if natural pollination is optimal (Williams, 1970). Lapins and Arndt (1974) reported that inadequate numbers and poor distribution of pollinizers was one of the main causes of poor fruit set. A ratio of four rows of 'Delicious' to one of pollinizer should be satisfactory in most situations but in colder locations with generally poor pollination conditions two rows of 'Delicious' and two rows of another variety could be a better arrangement. Roberts (1947) found that 'Delicious' trees at the edge of an orchard regularly had somewhat better set, as incoming bees brought pollen from a distance. He concluded that greater bee visitation is needed to set 'Delicious' than is required for most other varieties. He also suggested that 'Delicious' should be planted no more than one row away from a good compatible pollen source.

Pollen tube growth differs following cross- vs. self-pollination. Modlibowska (1945) observed 3 types of pollen tubes in apple and pear styles. 1) Incompatible tubes - these grow slowly and are inhibited earlier at 25 to 30°C than at 10-20°C; 2) Semi-compatible tubes - these tubes

grow slowly but unlike the completely incompatible tubes they do not stop growing completely; 3) Compatible tubes - the growth rate of tubes at 10-15°C is similar to that of those in classes 1 and 2, but is accelerated by a rise in temperature. Temperature affects the growth of incompatible tubes in the opposite way.

3. Pollenizing Agents

Pollination agents are important during bloom of apple. The chance of pollen transfer by wind is very low and fruit set is highly dependent upon insect activity and sources of viable pollen (Free, 1964). Apple pollen grains are sticky and dense and adhere tenaciously to one another, in contrast to the wind borne pollen of some plants. Robinson (1980) confirmed that wind played an insignificant role in pollination of apples by caging apple trees to exclude insects but permit wind transfer of pollen. Flowers did not set fruit even if bouquets of a pollinizing cultivar were suspended among the branches. Another obvious problem with wind pollination is that it is undirected. The "target area" (stigmatic surface) is very small on apple blossoms, and pollen must be transferred directly to the stigmas to be effective.

These facts leave insects as the main vector, particularly honey bees (Hoffman,1966, Wilson and Williams 1970). The number of honey bees per colony (about 30,000

at apple bloom) is huge in comparison with the number of other bees and they are easily moved in large numbers by commercial bee keepers. The colonies should be placed at points where they receive maximum sunlight and the sites should be well drained and protected from winds. One colony per acre is recommended (Robinson,1980).

4. Supplementary Pollination

Supplemental hand pollination is a potential method for enhancing fruit set, but the cost would probably be prohibitive. Williams (1970) investigated the effects of natural and supplementary hand pollination on fruit set of 'Cox's Orange Pippin' apple in England. He found that the average final set per 100 flower clusters for 21 'Cox's' orchards was 33.1 for branches receiving supplementary pollination (one flower hand pollinated per 4 clusters) vs. 25.6 for controls with natural pollination only. Supplementary pollination increased yield by an average of 29%. He concluded that orchards in which hand pollination is effective are deficient in bees, assuming suitable pollinizers and spacing. Kondrate'ev,et al.(1972) hand-pollinated apples, cv. Golden Winter Pearmain, and plum, cv. Tulew Gras, repeatedly at 6 to 72 hour intervals, and concluded that supplementary pollination speeded up fertilization and improved fruit set. However, they did not present data to support their conclusion. Increased fruit

set may have been the result of higher numbers of pollen grains per stigma. Forshey (1978) reported that the amount and timing of cross-pollination are critical. Theoretically only a few pollen grains per flower are required for fertilization. However, 'Delicious' flowers must be saturated with pollen because a relatively low percentage of pollen tubes actually reach the embryo sac. When post bloom weather is cool, slow pollen tube growth in combination with early degeneration of embryo sacs results in poor set. He demonstrated that receptivity of 'Delicious' flowers is not uniform throughout the bloom period and the effective pollination period may be limited to one or two days. However, he failed to factor out flower age.

Lapins and Arndt (1974) found a close relationship between the amount of pollen on the stigmas and final set. A low amount of pollen was found in cool areas and in dense orchards. They rated crop production from 1 to 10. In orchards with a high proportion of pollinizer, the rating was 6.0 whereas in orchards with insufficient pollinizers the rating was 1.5. They reported that less than about 50 pollen grains per stigma usually resulted in poor germination of pollen, slow growth of pollen tubes and low set of fruit. However, they did not present data to support this observation.

Another factor which may control pollen tube growth is double pollination. In an early report Cooper (1928)

indicated that when 'Delicious' pistils were pollinated with pollen from various cultivars, 'Ben Davis' pollen tubes were the longest, followed by 'Transparent', 'Jonathan', 'Stayman' (triploid) and 'Delicious'. Knight (1917) reported that pollen tubes make their way through the tissue along a more or less well-defined path which is accompanied by the decomposition of cells or extrusion of material from them. Visser and Verhaegh (1980) investigated the effect of two consecutive hand pollinations of 'Golden Delicious' flowers, as well as the separate effect of each, with the aid of mildew- or scab-resistant pollen donors. The flowers were either pollinated once or twice at intervals of one or two days, the seeds were harvested from the fruits obtained, and the seedlings evaluated for disease resistance. They found that double pollination with the same pollen had a similar effect on fruit and/or seed development as a double pollination with pollen from two different cultivars. In all trials an average of 37% of the seeds originated from the first and 63% from the second pollination. They concluded that pollen tubes grew more rapidly in styles which had been previously penetrated by pollen tubes.

C. Ovule Longevity

Ovule longevity may also be an important factor in 'Delicious' fruit set. Hough (1947) reported that in ovules of 'Delicious' the most frequent abnormality was

either a tardy initiation of the megaspore mother cell or a slower rate of development of the megaspores and embryo sac. Such retarded embryo sacs would seldom be expected to develop into fully differentiated eight nucleate embryo sacs in time for fertilization, especially if their development continued to be at a slower than normal rate. Other apparently normal embryo sacs broke down soon after the flower opened, even though the flowers had been pollinated with compatible pollen. Hartman and Howlett (1954) found that a considerable percentage of 'Delicious' embryo sacs were delayed in development or showed signs of premature degeneration and the percentage increased markedly after 72 hours. When pollination was delayed until 48 hours after anthesis fertilization was greatly reduced. They attributed this largely to the early ovule degeneration. Forshey (1978) stated that a significant proportion of 'Delicious' flowers are not viable; however, he did not present supporting data. In some nonviable flowers the embryo sac is immature at bloom, while in others early degeneration of the embryo sac excludes the possibility of fertilization.

Rootstock may have an effect on embryo sac degeneration in 'Delicious'. Marro (1976) made a comparison of fruit set of 'Richared Delicious' apple trees on seedling vs. M9 rootstock. Flowers were hand pollinated at petal opening, full bloom and petal fall. Embryo sac degeneration was observed in a certain percentage of flowers pollinated at

full bloom but was greater at petal fall. On both dates embryo sac degeneration was greater on the seedling rootstock.

Williams (1970) studied the relationship between flower fertility and fruit set in 'Cox's Orange Pippin'. He termed the period during which pollination results in fertilization the "effective pollination period" (E.P.P.). E.P.P. is a function of ovule longevity and rate of pollen tube growth. Some flower clusters were pollinated on the day the flower opened (day 0), others 2, 4, or 6 days later. The results of this study indicated that the effectiveness of pollination decreased over the period investigated. The E.P.P. of various apple cultivars ranged from 2 to 3 days to 8 to 10 days after anthesis (Williams, 1965a). Temperature during anthesis influences the length of the E.P.P. because of its effect on both tube growth and ovule longevity.

D. Ethylene

Greene (1980) reported that application of aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, increased set and reduced ethylene evolution in apple flowers. He suggested that because exogenous ethylene induces abscission, endogenous levels of ethylene in apple flowers may reduce fruit set. Williams (1980) applied AVG to spur 'Delicious' trees at 450 ppm prior to harvest in 1979. In the spring of 1980, ethylene evolution from buds

treated with AVG was lower than for control buds. This supports Greene's suggestion. However, neither investigator applied ethylene generating compounds such as ethephon at full bloom to determine their effects on fruit set.

The role of ethylene in fruit set is discussed more fully in the following sections on the biosynthesis and physiological effects of this hormone.

III. Physiology and Biochemistry of Ethylene

A. Ethylene as a Plant Hormone

Evidence for the role of ethylene as a naturally-occurring plant hormone has accumulated over several decades (Leopold and Kriedemann, 1975). Neljubow (1901) was first to report that ethylene regulated the growth and development of plants. He observed that pea seedlings germinated in the lab grew in a horizontal direction. However, plants grown in air drawn from outside the lab grew normally in a vertical fashion. By adding illuminating gas to outside air he obtained the same growth phenomenon observed with laboratory air. He suspected that the hydrocarbon content of illuminating gas was the active factor. Laboratory air passed through a CuO ignition tube lost its ability to alter the growth of pea seedlings. Neljubow examined a number of the compounds of coal gas for their effects on plants. SO_2, CS_2, benzol, xylol, and naphthalene caused injury and inhibited growth, but only acetylene and ethylene induced

horizontal growth.

The initial suggestion that plants produced ethylene came from the report of Cousins in 1910. He observed that oranges produced a gas that promoted the ripening of bananas. Denny (1924) found ethylene to be the active component in combustion fumes which induced fruit ripening. Gane (1934) proved chemically that apple fruits produced ethylene. Denny and Miller (1935) exploited this idea and presented evidence for ethylene production not only by ripening fruits but also by flowers, seeds, leaves and even roots.

Ethylene is a natural plant hormone because it is a product of plant metabolism, acts in trace amounts, and is neither a substrate nor cofactor in reactions associated with major plant developmental processes (Lieberman, 1979). Using very sensitive instruments and very careful techniques, it is possible to show that ethylene is an endogenous growth regulator in plants, and that it is present in fruits from the earliest stages of development (Pratt and Goeschl, 1969). The advent of the gas chromatograph in the early 1960's allowed a rapid, sensitive and simple assay of ethylene evolved by plant tissue without extraction or purification prior to analysis. At the present time ethylene is recognized as a powerful natural regulating substance in plant metabolism, acting and interacting with other recognized plant hormones in trace amounts, and its

effects are observed especially during critical periods in the life cycle of higher plants (Lieberman, 1979). Yang (1980) proposed that due to its gaseous nature, ethylene exerts a physiological effect at or near a site where it is synthesized. For this reason the classical definition of a hormone (action at a distance from the source) does not apply to ethylene. However, 1-aminocyclopropane-1-carboxylic acid (ACC) synthesized in one part of the plant may exert its effect through conversion to ethylene in another part of the plant (Yang, 1980).

B. Ethylene Biosynthesis

1. Biochemical Pathway

Methionine was first suggested as a possible precursor of ethylene in climacteric fruits such as apple (Lieberman, et al. 1965, 1966), banana (Burg and Clagett, 1967) and avocado (Baur, et al. 1971) and this was proven by Yang (1974). Carbon 1 of methionine is converted to CO_2 when radioactive methionine is fed to plant tissue (Burg and Clagett, 1967), C_2 to formic acid (Siebert and Clagett, 1969), Carbon 3 and 4 to ethylene (Baur, et al. 1971; Hanson and Kende 1976) and CH_3-S remains in the tissue (Adams and Young, 1977; Burg and Clagett, 1967). Adams and Yang (1977, 1979) identified 5-adenosylmethionine (SAM) and 1-amino-cyclopropane-1-carboxylic acid (ACC) as intermediates in the pathway from

methionine to ethylene and proposed the following sequence for the pathway of ethylene biosynthesis in apple tissue: methionine → SAM → ACC → ethylene. Identification of SAM as an intermediate indicates that methionine must be activated by ATP and methionine adenosyltransferase (Adams and Yang, 1977; Konze and Kende, 1979; Lieberman, 1979).

The conversion of 5-adenosylmethionine (SAM) to 1-aminocyclopropane-1-carboxylic acid (ACC) by ACC synthase (Adams and Yang, 1979; Boller, et al., 1979; Yu, et al., 1979), requires pyridoxal phosphate. The methylthio (CH_3-S) group is split off at this point and is incorporated into 5'-methylthioadenosine (MTA), which is converted to 5'-methylthioriboside (MTR). MTR is converted back to methionine by combining with a 4-carbon acceptor such as homoserine. This is an important step because many tissues do not contain high enough levels of methionine to maintain a high rate of C_2H_4 production unless the S atom is recycled (Herner, 1981).

The third step is conversion of ACC to C_2H_4, for which oxygen is required (Adams and Yang, 1979; Lonze and Kende, 1979).

2. Factors Affecting Rate of Ethylene Biosynthesis

a. Carbon dioxide - Several environmental factors affect ethylene production. Depending on the tissue, CO_2 can inhibit, promote, or have no effect on ethylene production. CO_2 concentrations between 10% (Potter and Griffiths,

1947) and 80% (Burg and Thimann, 1959) inhibited ethylene production in mature apple fruit tissue. However, the effect may have been indirect via the inhibition of ripening by CO_2. The effect of CO_2 on overcoming or blocking the action of ethylene was noted as early as 1927. Mack (1927) observed that the addition of CO_2 to the gas phase of ethylene reduced the ability of ethylene to blanch celery. After discovery of the blocking effect of CO_2 on ethylene action, CO_2 was found to be a competitive inhibitor of ethylene action. Burg and Burg (1965, 1967) observed that CO_2 is a close structural analogue of allene, a compound which substitutes for ethylene in both the pea section growth assay and in fruit ripening.

$O=C=O$	$CH_2=C=CH_2$	$CH_2=CH_2$
carbon dioxide	allene	ethylene

Because CO_2 has the structural features needed for ethylene action, except that it lacks the terminal carbon atom and is negatively charged on both ends, it could act as a competitive inhibitor of ethylene action. They tested this possibility by measuring the growth of pea stem sections in the presence of differing concentrations of CO_2 and ethylene. Concentrations of less than 1.8% CO_2 competitively inhibited the action of ethylene. The affinity of ethylene for the receptor site is one million-fold greater than that of CO_2;

therefore, if enough ethylene is present CO_2 will not prevent its action.

Imaseki, et al. (1968) observed that removal of CO_2 by KOH reduced ethylene production by sweet potato roots and suggested that CO_2 stimulated ethylene synthesis. However, CO_2 has no effect on ethylene production by citrus fruits (Ben-Yehoshua and Eaks, 1969; Rasmussen and Jones, 1969).

b. Oxygen. The oxygen level also affects ethylene production. The inhibition of ethylene production by low oxygen levels or anaerobiosis has been reported by many workers for a variety of tissues (Baur, et al., 1971; Burg and Thimann, 1959; Curtis, 1969, Haber, 1926). Burg and Thimann (1959) showed that the effect of oxygen on ethylene production in apple sections is similar to its effect on respiration, and suggested that ethylene production is dependent on respiration. Apple sections stopped producing ethylene soon after being placed in nitrogen. When the sections were returned to air, ethylene production resumed immediately at a greater rate than that of the controls. Burg and Burg (1967) showed that attachment of ethylene to the receptor is enhanced by O_2 and this mechanism can be inhibited by CO. An ethylene precursor may accumulate in the tissue under anaerobic conditions; this precursor may rapidly be converted into ethylene in the

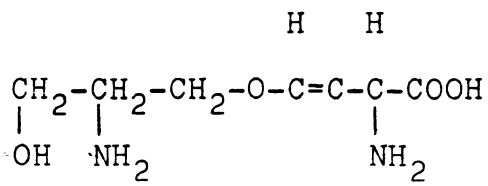
presence of oxygen (Abeles, 1973). Adams and Yang (1979) showed that oxygen is required for conversion of ACC to ethylene.

c. Temperature. The optimum temperature for ethylene production by apple is 30°C (Burg and Thimann, 1959; Hansen, 1945; Burg, 1962; Yu, et al., 1980). As temperature increases above 30°C the rate of ethylene production falls, ceasing entirely at 40° (Burg, 1962). Yu, et al., (1980) found that increasing the temperature to 35° caused 1-aminocyclopropane-1-carboxylic acid (ACC) to accumulate, while reducing the rate of ethylene production. They suggested that the conversion of ACC to ethylene can be inhibited by high temperature.

d. Chemical inhibitors. Uncouplers of oxidative phosphorylation, such as 2,4-dinitrophenol (DNP), carbonyl cyanide m-chlorophenylhydrazone (CCCP) and CO^{2+}, drastically reduced both ATP and C_2H_5 production, presumably by inhibiting the step from methionine to SAM (Burg, 1973; Murr and Yang, 1975; Apelbaum, et al., 1981). However, if this step is the only one inhibited, adding 1-aminocyclopropane-1-carboxylic acid (ACC) should overcome the inhibition by DNP and CCCP (Herner 1981).

Several analogues of enol ether amino acids inhibit ethylene production. Owen and Wright (1965) extracted

L-2- amino-4-(2-amino-3-hydroxypropoxy)-trans-3-butanoic acid (rhizobiotoine) with the structure



from pure cultures of certain strains of the soybean root nodule bacterium, Rhizobium japonicum. Owen, et al. (1971) reported that this compound inhibited ethylene production about 75% in both intact sorghum seedlings and senescent apple fruit tissue slices. Although addition of methionine failed to overcome the inhibition completely in either system, it reduced the level of inhibition from 75% to 60%. They concluded that rhizobitoxine may block (a) the biosynthesis of methionine, (b) the conversion of methionine to ethylene or (c) both. Scannel, et al. (1972) isolated methoxyvinylglycine from the fermentation broth of Pseudomonas aeruginosa AT_{cc}-7700. In 1974 Pruess, et al. isolated a third inhibitor L-2-amino-4-(2-aminoethoxy)-trans-3-butanoic acid or aminoethoxyvinylglycine (AVG), from a fermentation broth of an unidentified species of Streptomyces sp. X-11-085. AVG differs from rhizobitoxine only by the loss of the terminal methoxyl group. The structural similarities between these amino acid analogues and methionine suggest that they may be competitive inhibitors for

the substrate attachment site of the ethylene forming enzyme system. AVG and its analogues inhibit many pyridoxal enzymes, and conversion of SAM to ACC *in vivo* is greatly inhibited by AVG (Yang, 1980). Therefore Adams and Yang (1979) proposed that the enzyme catalyzing the conversion of SAM to ACC is a pyridoxal enzyme. Boller, et al. (1979) observed that AVG at low concentrations inhibited the action of ACC-synthase isolated from tomato fruit tissue (Ki = 0.2 μM), but did not inhibit ethylene production from ACC.

e. Auxin as a stimulator of ethylene synthesis. A number of investigators have reported that auxin stimulates ethylene production which in turn induces premature abscission of leaves and other organs. Zimmerman and Wilcoxon (1935) observed that treatment of tomato plants with auxin stimulated evolution of a gas which caused epinasty. Later Morgan and Hall (1962) presented evidence that this gas was ethylene. Abeles and Rubinstein (1964) found that auxin application stimulated ethylene production from roots, stems and leaves of several genera and that the endogenous level of auxin also appeared to regulate the production of ethylene from vegetative tissue. IAA treatment of mung bean hypocotyls increased ethylene production 500-fold and stimulated conversion of methionine to ethylene. Yang (1980) suggested that auxin stimulates ethylene production

by inducing the synthesis of ACC synthase. Yu and Yang (1979) found that IAA stimulated ACC synthase activity and showed that conversion of SAM to ACC is the rate controlling step in ethylene production.

C. Ethylene Generators

Ethylene gas is difficult to apply under field conditions. This limitation was overcome by the development of ethylene releasing compounds which can be applied as sprays, the most important commercial compound being 2-chloroethylphosphonic acid (ethephon or CEPA) (deWilde, 1971). Kabachnik and Rassuskaya (1946) described the synthesis of ethephon and Mayard and Swan (1963) reported the generation of ethylene from this compound. Warner and Leopold (1967) were the first investigators to report its use as a plant regulator.

Ethephon is stable in the acid form but breaks down at a pH of 3.5 or above (Abeles, 1973). The pH of the cytoplasm of plant cells is generally greater than 4, so the growth regulating activity of ethephon has been attributed primarily to its ability to release ethylene within the tissue (Morgan, 1969; Warner and Leopold, 1969). Plant tissues of different acidity might be expected to show different capacities for ethylene evolution. Warner and Leopold (1969) showed that leaves from Bryophyllum plants grown under long photoperiods produced substantially more

ethylene after treatment with CEPA than leaves from plants grown under short photoperiods. This could be expected from the relatively higher pH of sap from the former (pH 4.6 and 4.0, respectively). Temperature has a significant effect on the rate of ethylene evolution from ethephon. Olien and Bukovac (1978) incubated the apical segments of one-year-old sour cherry shoots in test tubes at 20, 30 or 40°C. Endogenous ethylene production increased with temperature up to about 30°, but the effect was small compared with the effect of temperature on release of ethylene from ethephon. The optimum temperature range for ethylene evolution from ethephon is 16° to 29° (Amchem Products, Inc., 1969).

D. Inhibitors of Ethylene Action

The biological action of ethylene can be overcome by silver ion. Spraying pea seedlings with silver nitrate effectively blocks the ability of exogeneously applied ethylene to induce the classical "triple" response -- growth retardation, stem swelling and horizontal growth. $AgNO_3$ blocks ethylene stimulated leaf abscission in cotton (Beyer, 1976). Spraying or momentarily dipping carnation flower heads in $AgNO_3$ solution (50-100 ppm) extended the life of cut flowers and counteracted the enhancing effect of ethephon on senescence (Halevy and Kofranek, 1977). Saltveit, et al. (1978) observed that infiltration of apple cortical

cylinders or banana fruit slices with solutions of $AgNO_3$ (0.03 mM or greater) significantly reduced ethylene production. On the other hand, cuttings of sweet potato treated with Ag^+ (250 to 2500 ppm) produced more ethylene than did controls (Walker, et al., 1979). Beyer (1979) showed that Ag^+ (100 ppm) was clearly the most potent antiethylene treatment of several tested on pea. However, 'Delicious' apple flowers treated with silver nitrate (20 and 200 ppm) produced more ethylene than did control flowers (Greene, 1980).

The mechanism of inhibition of ethylene action by Ag^+ has been studied by several investigators. The data of Burg and Burg (1967) suggest that the activity of ethylene requires binding to a metal. Ethylene, like other unsaturated aliphatic compounds, forms complexes with metals, including copper (Coates, et al., 1968). Month-old zinc-deficient tomato plants respond very little to ethylene even when exposed overnight, whereas plants deficient in copper, iron, phosphorus or nitrogen show strong epinasty within a few hours (Burg and Burg, 1967). Beyer (1976) suggested that Ag^+ may substitute for Cu^+, thereby interfering with ethylene oxidation, and hence ethylene action. Because Ag^+ and Cu^+ have the same valence, are similar in size, and both form complexes with ethylene, Ag^+ might interfere with the binding of ethylene to Cu^+. Walker, et al. (1979) suggested that Ag^+ blocks the C_2H_4 activation site and thereby interferes with autocatalytic regulation of C_2H_4 production.

IV. Evidence for the Role of Ethylene in Fruit Set

A. Ethylene Production by Flowers and Fruits

1. Effect of Pollination

Pollinated flowers of cotton (Lipe and Morgan, 1973) and carnation (Nichols 1971, 1977) produced more ethylene than unpollinated flowers. Over half of the ethylene produced by one-day-old cotton flowers is released by the combined stigma, style, and stamens (Lipe and Morgan, 1973). Burg and Dijkman (1967) observed an increase in ethylene evolution within 8 to 10 hours after pollination and flower fading in orchid. The response was duplicated by applying IAA (5 mM). They concluded that release of pollen auxin in the stigma, and its diffusion to the column and lip, induced ethylene formation in these tissues, leading to floral fading. Hall and Forsyth (1967) measured ethylene production by flowers of strawberry and lowbush blueberry following pollination. Twenty-four hours after pollination pollinated flowers produced greater amounts of ethylene than non-pollinated flowers of the same age in each of the two species. The amount of ethylene produced following self-pollination was not significantly different from that following cross-pollination. Over 90% of the ethylene produced by blueberry flowers came from the style and the stigma. They concluded that pollination may stimulate IAA formation leading to an increase in ethylene production. In banana

the rate of ethylene production is greater in flowers having an abscising perianth than in those with a persistent perianth (Israeli and Blumenfeld, 1980). Plich (1977) measured ethylene evolution from strawberry beginning the first day of flower opening and continuing until a few days after petal fall. He found abscission of petals in strawberry to be dependent on pollination, because pollination did not induce C_2H_4 evolution. Nicholas (1977) observed that most of the ethylene was evolved from the style and petals in carnation; pollination of intact flowers promoted endogenous ethylene production and accelerated petal wilting. He suggested that pollination accelerates petal wilting, stimulates ethylene production in all flower tissues and induces ovary growth. Approximately 40-50% of the ethylene could be accounted for by the styles and most of the remainder by the petals. Since the styles contribute less than 4% of fresh weight of the flowers, they are the most active center of ethylene production. Blanpied (1972) found that ethylene content of 'Golden Delicious' apple flowers increased as flowers developed. The level of ethylene increased from pink stage to petal fall, then decreased as fruit development began; however, ethylene content remained high in unpollinated flowers which abscised. In 'McIntosh' flower buds ethylene content increased from green tip to tight cluster stage. In sweet and tart cherry ethylene content was high at half green calyx, declined

rapidly to green calyx, then declined slowly until petal fall. Abscised flowers of both apple and cherry contained more ethylene than adhering flowers. Abscising and adhering fruits of 'Golden Delicious', 'Red Astrahan', 'Delicious', and 'McIntosh' were collected and ethylene extracted from them during the period of "June" drop in two seasons. The fruit pedicel contained 3- to 10-fold more ethylene per unit weight than fruit tissue, but tissues of abscising fruits did not consistently contain more ethylene than similar tissues of adhering fruits.

2. Effects of Auxins

Synthetic auxins such as naphthalene acetic acid and its derivatives have been used as thinning agents in apple for many years. Davidson, et al. (1945) first showed that NAA could be used as a post-bloom spray. They obtained effective thinning when apple trees were sprayed two to three weeks after bloom.

Several theories have been suggested to explain the action of NAA in apple fruit thinning. Luckwill (1953) proposed that NAA thins by inducing seed abortion. Later Luckwill and Lloyd-Jones (1962) showed that only 0.2% of the ^{14}C-NAA applied to apple leaves was recovered from the seed after 5 days and none of it was in the form of unmetabolized NAA. They concluded that seed abortion and consequent abscission of the fruitlet is not due to the

direct action of NAA itself but rather to the effect of a breakdown product which has no auxin-like properties.

The mechanism of action of NAA is still not well understood. One hypothesis is that application of NAA stimulates C_2H_4 synthesis, and the ethylene produced induces abscission of immature fruits.

Schneider (1975) found that spraying with NAA 4 days after petal fall caused ethylene evolution in leaves, fruits and pedicels of 'Golden Delicious', 'Staymared' and 'Red Rome' apple sampled 24 hours and 48 hours after spraying. Walsh et al. (1979) sprayed 'Golden Delicious' and 'Northern Spy' with 15 ppm NAA two weeks after petal fall. Twenty hours after application ethylene evolution from 'Golden Delicious' spurs treated with 15 ppm was 5 times greater than that from control spurs. Significant differences between control and NAA-treated spurs were still evident in both cultivars 2.5 days after treatment.

B. Effects of Ethylene-Generating Compounds

1. Effects on Initial Set

Ethylene reduces set when applied prior to or during bloom (Table 2). Apple fruit set was greatly reduced after applying 200 to 2000 ppm ethephon in the spring at late dormant, pink bud, full bloom and post-bloom stages of development (Amchem Products, Inc., 1969). Edgerton and

Table 2. Effects of ethephon on apple fruit set when applied prior to or during bloom.

Reference	Stage of development	Conc. (ppm)	Fruits/100 clusters	Cultivar
Edgerton & Greenhalgh (1969)	Delayed dormant	0	36.2	McIntosh
	" "	200	4.6	
	" "	2000	0.0	
	Pink	0	31.4	
	"	200	10.1	
	"	2000	0.0	
	Full bloom	0	28.3	
	" "	1000	2.9	
	Pink	0	37.3	R. I. Greening
	"	200	19.3	
	"	2000	0.0	
Veinbrants (1979)	Full Bloom	100	(adequately thinned)	Richared Delicious Starkrimson Delicious
Kustermans & Westlaken (1978)	Full bloom	2000	(over thinned)	Winston
Wertheim (1978)	10% bloom	2000	(good response)	Benoni
	" "	3000		
	" "	250	(overthinned)	Lombartscalville

Greenhalgh (1969) applied ethephon to 3 apple cultivars at several stages of development from prebloom to harvest. Foliar sprays of ethephon at 200 and 2000 ppm during dormant and pink bud stages significantly reduced fruit set at 200 ppm and eliminated it in 'McIntosh' at 2000 ppm. Application at 1000 to 2000 ppm during the prebloom to early postbloom stages on 'McIntosh', 'Early McIntosh' and 'R.I. Greening' apple completely eliminated all fruit with little or no phytotoxicity (Edgerton and Greenhalgh, 1969; deWilde, 1971). Veinbrants (1979) applied ethephon at 100 ppm at or shortly after full bloom on several apple cultivars. 'Golden Delicious', 'Gravenstein' and 'Jonathan' were thinned adequately when followed by NAA (7.5 ppm). On lighter setting 'Richared Delicious' and 'Starkrimson Delicious' ethephon at 100 ppm resulted in adequate thinning when applied at or shortly after full bloom. Kustermans and Westerlaken (1978) compared hand thinning vs. ethephon treatment on the yield of 'Winston' apple. Ethephon at 2000 ppm applied at full bloom over thinned and reduced yield.

2. Effect on "June" Drop

Effects of ethephon upon fruitlet abscission vary with concentration and time of application (Table 3). When applied 10 days after full bloom ethephon at 50 ppm had no effect on final set of 'McIntosh' but 250 and 500 ppm

Table 3. Effects of ethephon on apple fruitlet abscission when applied at various times after full bloom.

Reference	Time of application (days after full bloom)	Conc. (ppm)	Fruits/100 clusters	Cultivar
Edgerton & Greenhalgh (1969)	10	0	28.0	McIntosh
	10	50	29.0	
	10	250	10.6	
	10	500	5.8	
	28	0	32.6	
	28	250	30.5	
	44	0	31.7	
	44	75	29.8	
	44	250	33.6	
	13	0	70.2	E. McIntosh
	13	50	54.5	
	13	150	13.6	
	13	450	0.0	
Walsh, et al. (1979)	14	0	54.0	Northern Spy
	14	100	13.6	
	14	200	2.2	
	14	0	43.4	Golden
	14	100	37.6	Delicious
	14	200	23.9	
Lord, et al. (1975)	26	0	61	Cortland
	26	1000	2	
	35	0	86	Mutsu
	35	250	73	
	35	500	7	
	44	250	79	
	44	500	22	

Table 3. Continued.

Reference	Time of application (days after full bloom)	Conc. (ppm)	Fruits/100 clusters	Cultivar
Veinbrants (1979)	35, 36, 42	200 to 400	Fruit eliminated	Jonathan, Richared,, Delicious and Gravenstein

significantly reduced final set (Edgerton and Greenhalgh, 1969). Concentrations of 75 or 250 applied 28 and 44 days after full bloom had no significant effect. 'Early McIntosh' responded to as little as 50 ppm applied 13 days after bloom, and 450 ppm removed all fruits. Concentrations of 200 to 400 ppm applied 35, 36 and 42 days after full bloom eliminated all fruits on 'Jonathan', 'Richared Delicious', and 'Gravenstein' in Australia (Veinbrants, 1979). Virtually all fruits abscised on 'Cortland' apple when ethephon at 1000 ppm was applied alone or with 1000 ppm Alar-85 26 days after full bloom (Lord, et al., 1973). Ethephon at 250 ppm had little effect on 'Mutsu' when applied 35 or 44 days after full bloom; 500 ppm was much more effective at 35 than 44 days. Ebert (1980) applied ethephon at 711 ppm 10 and 12 days after full bloom to 'Golden Delicious' and 'Goldparmane' apple fruitlets, respectively. Abscission was not affected in 1977, but was stimulated in 1978.

C. Effects of Inhibitors of Ethylene Biosynthesis

Because ethylene induces flower abscission, Greene (1980) suggested that endogenous ethylene levels may be sufficiently high in apple flowers to limit fruit set. Application of AVG increases fruit set in some fruits, thus providing support to this hypothesis. Dennis, et al. (1978) applied an aqueous spray of AVG at 0, 2500, 5000

and 10,000 ppm to swelling buds of apple, cherry and plum. Fruit set of apple was increased 20 to 50% but differences were not significant at the 5% level. Archbold and Dennis (unpublished) reported that fruit set of several cvs. of apple was significantly increased by AVG applied at full bloom at 200 and 500 ppm. Maag (1979) increased fruit set in 'Golden Delicious' apples by spraying early in the spring with 200, 600 and 2,000 ppm of AVG, although 200 ppm was slightly less effective. Concentrations above 3,000 ppm often resulted in severe phytotoxicity. Greene (1980) applied AVG to 'Richared Delicious' apples at full bloom and one day after full bloom. A concentration of 200 ppm significantly increased fruit set, while greatly reducing ethylene production. The inhibitory effect of AVG on ethylene production had dissipated 15 days after treatment. AVG had no effect on viable seeds per fruit. AVG completely overcame GA_{4+7}- and BA-induced ethylene production, reducing it to a level similar to that in the AVG treatment alone. Williams (1980a) applied 1000 ppm AVG to 15-year-old 'Delicious' and 'Golden Delicious' apple trees 2 weeks after full bloom and increased fruit set in both varieties. He also reported that AVG can increase cropping in winter pear trees either by preventing abscission or by increasing fruit set. He also reported that AVG stimulated lateral branching. However, AVG reduced fruit set in cherry and plum (Archbold and Dennis, unpublished; Vecino and Dennis, unpublished).

AVG also increases fruit set in other crops, such as bean, and inhibits ethylene production in cucumber. Natti and Loy (1978) reported that emasculation of hand pollinated muskmelon flowers reduced fruit set in comparison with open pollination. AVG applied to the base of the calyx of perfect flowers improved fruit set following emasculation; IAA alone improved fruit set slightly, and IAA + AVG were more effective than IAA alone, but less effective than AVG alone at optimum dosage. Foliar application of AVG at 20 or 60 ppm to 2-week-old bean seedlings stimulated growth and fruit set (Shanks, 1980). Application of AVG to soybean delayed leaf senescence, stimulated photosynthetic rate and increased yield about 14% (deSilva, personal communication).

D. Effects of Inhibitors of Ethylene Action

Silver nitrate inhibits ethylene action, possibly by competing with ethylene's metabolic binding site (Beyer, 1976, 1979). Spraying explants of 'Sprinter Scarlet' geranium inflorescences with silver nitrate effectively reduced petal abscission and slightly promoted ethylene synthesis (Miranda, 1981). Silver thiosulfate was more effective and less phytotoxic. 'Delicious' apple flowers treated with $AgNO_3$ produced more ethylene than control flowers, but the effect was not significant (Greene, 1980). The same author reported that $AgNO_3$ had no effect on fruit

set and injured flowers when used at high concentrations (200 ppm). Applying $AgNO_3$ at 50 to 200 ppm at full bloom to flowers of three apple cultivars ('Wealthy', 'Golden Delicious', and 'Jonathan') had no effect on fruit set (Archbold and Dennis unpublished data).

SUMMARY

Yields of of 'Delicious' apple are relatively low compared with those of other cultivars. Several reasons have been proposed for this including greater susceptibility of flowers to frost injury, limited ovule longevity, slow growth of pollen tubes in the style, "basal gaps" between stamen filaments which permit bees to extract nectar without pollinating the stigma, low temperature, solar radiation during and immediately after bloom, and high level of endogenous ethylene. These factors may act individually or together to reduce yield in this cultivar.

The role of ethylene in apple fruitset has not been critically evaluated. Because AVG both reduces ethylene production and increases fruit set investigators have assumed the later is a result of the former. However, no studies are known in which cultivar effects on the rate of ethylene production have been examined. Nor have the quantitative effects of chemicals on both set and ethylene production have been carefully compared. AVG may exert other effects such as delay of embryo abortion which are

more important than its effect on ethylene synthesis. Similarly, although apple fruits which abscise in the "June" drop produce more ethylene than those which do not, and thinning chemicals generally stimulate ethylene production, a causal relationship has not been established between ethylene production and abscission.

Likewise, the hypothesis that basal gaps limit set in the 'Delicious' has not been adequately tested. If this factor is important, why does 'Northern Spy', which exhibits the same characteristics, set so heavily that it is biennial? One way of testing the hypothesis would be to hand pollinate open-pollinated flowers of both 'Delicious' and a cultivar which does not have basal gaps, such as 'McIntosh'. If the increase in set is greater in the former than the latter, basal gaps would appear to be an important factor in limiting yield.

Some of these approaches were used in studies reported in this thesis.

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SECTION I

THE ROLE OF ETHYLENE IN FRUIT SET OF APPLE

Abstract. Branch sprays of (2-chloroethyl)phosphonic acid (ethephon), an ethylene generating compound, and aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, were applied at full bloom to limbs of 'McIntosh', 'Red Prince', 'Delicious' and 'Golden Delicious' apple (Malus domestica Borkh.) to determine their effects on fruit set and ethylene evolution. AVG significantly increased fruit set in all cultivars when used at 200 ppm; at 100 ppm its effects were generally not statistically significant. AVG tended to reduce ethylene evolution from flowers excised 1 to 10 days after treatment, but the reduction was small and not statistically significant. Ethephon (40 and 80 ppm) did not affect fruit set significantly, yet markedly increased ethylene production. Evolution of ethylene from ethephon-treated flowers was considerably lower in 'Delicious' than in the other two cultivars. AVG had no effect on length: diameter (L/D) ratio and seed number but reduced fruit weight. Ethephon had no effect on fruit weight, seed number or L/D ratio. Based upon these observations the promotive effect of AVG on fruit set does not appear to be dependent upon its ability to inhibit ethylene synthesis.

'Delicious' was recognized as a light bearing cultivar as early as 1928 (Howlett, 1928). Several factors may be associated with poor fruit set in 'Delicious'. Frost susceptibility is one of the causes of poor cropping, for 'Delicious' flowers are more susceptible than many other cultivars (Hartman and Howlett, 1954; Roberts, 1946; Meader and Blasberg, 1946; Westwood, et al., 1976). Solar radiation and temperature also may affect set; Gardener, et al. (1949) reported that fruit set of 'Delicious' was positively correlated with high radiant energy and high temperatures shortly after full bloom. However, Dennis (1979) analyzed their data and found that correlation coefficients were low and not statistically significant. Flower structure is another factor which has been proposed as the cause of poor set of 'Delicious'. Both Roberts (1945) and Robinson (1980) reported that the structure of 'Delicious' flowers permits honey bees to remove nectar without pollinating the stigma. Both investigators observed "sideworking" of honey bees on 'Delicious' blossoms as a result of "basal gaps", or spaces between stamens.

Ethylene is a naturally occurring plant hormone (Leopold and Kriedemann, 1975) which is involved in flower and fruit senescence and abscission. Application of ethylene directly or indirectly induces flower and fruit abscission (Abeles, 1973). Ethylene biosynthesis in flowers is stimulated by pollination in cotton (Lipe and Morgan, 1973),

blueberry (Hall and Forsyth, 1967), and carnation (Nichols, 1977). In grape the endogenous level of ethylene rises at full bloom, falls at fruit set, then declines during berry development (Singh and Weaver, 1976). Ethylene content of apple flowers increases as flowers develop, then declines as the fruitlets enlarge (Blanpied, 1972).

Application at full bloom of aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, increased fruit set and reduced ethylene evolution in apple flowers (Greene, 1980). Application of AVG to 'Delicious' apple trees prior to harvest reduced ethylene evolution from opening buds the following spring, and increased fruit set (Williams, 1980). The compound also increased fruit set in bean (Shanks, 1978) and muskmelon (Natti and Loy, 1978). A synergistic effect was found between AVG and promalin, a commercial mixture of N-6-benzyladenine (BA) and gibberellins 4 and 7 (GA_{4+7}), on fruit set of 'Delicious' (Greene, 1980). However Dennis (unpublished data) observed that promalin reduced set of 'Red Prince Delicious' when used alone and did not act synergistically with AVG on fruit set. P. B. Lombard (1981) applied AVG at 150, 300 and 600 ppm to 7-year-old 'Comice' pear trees at full bloom and at various times thereafter. Fruit set was increased at all concentrations, but the increase was statistically significant only at 600 ppm.

Ethephon ((2-chloroethyl)phosphonic acid) is an

ethylene generating compound which releases ethylene within the treated tissues (Morgan, 1969; Warner and Leopold, 1969). The effect of ethephon on fruit set depends on concentration and stage of flower bud development (Edgerton and Greenhalgh, 1969). When ethephon was applied to 3 apple cultivars during dormant and pink bud stages, 200 ppm significantly reduced fruit set and 2000 ppm eliminated it in 'McIntosh' (Edgerton and Greenhalgh, 1969). Application at 1000 to 2000 ppm during the prebloom to early postbloom stages on 'McIntosh', 'Early McIntosh' and 'R. I. Greening' apple completely eliminated all fruit with little or no phytotoxicity (Edgerton and Greenhalgh, 1969; deWilde, 1971).

Greene (1980) hypothesized that the promotive effect of AVG on apple fruit set was due to its inhibition of ethylene synthesis. This hypothesis implies that the rate of ethylene synthesis is a limiting factor in fruit set under natural conditions. The purpose of this study was to determine if ethylene production by apple flowers does indeed limit set.

Materials and Methods

Experimental procedure, 1980. Aqueous sprays of AVG or ethephon were applied to branch units of 14-year-old trees of 3 apple cultivars, 'McIntosh', 'Red Prince Delicious',

and 'Golden Delicious', at the Horticultural Research Center, East Lansing, Michigan. Five uniform limbs per tree on four mature trees of each cultivar were selected and 75 to 100 flower clusters were counted on each branch at the pink stage. The first 50 clusters were used to evaluate fruit set and development; the remainder were used to measure ethylene evolution. The following solutions containing 0.1% Tween 20 as a wetting agent were applied at full bloom (May 14, 16, and 19, for 'McIntosh', 'Delicious' and 'Golden Delicious', respectively), using a randomized block design with trees as blocks: wetting agent only; AVG at 100 or 200 ppm; ethephone at 40 or 80 ppm.

Fruit set was recorded before and after "June drop" and two flower clusters were removed from each branch at intervals of 1 to 10 days after treatment to measure ethylene evolution. The clusters were held with their bases in water in sealed 135 ml containers in the dark at 21°C, and CO_2 was absorbed by placing a filter paper wick moistened with 40% KOH in each container. The jars were ventilated after 4 hr and ethylene accumulation was monitored by removing a one ml gas sample through a serum cap after an additional 4 hr. Ethylene was determined using a gas chromatograph (Varian Aerograph Series 1700 or 1400), equipped with a flame ionization detector. A column (45 x 0.32 cm) of 60 to 80 mesh Al_2O_3 was used at 60° or 80°C. The amount of ethylene in samples was calculated by the following

formula:

$$C_2H_4{}_s \ (\mu\ell \cdot g^{-1} \cdot hr^{-1}) = \frac{C_2H_4{}_{st} \text{ (ppm)} \times PH_s \times \text{vol. } (\ell)}{ATT_{st} \times PH_{st} \times wt_s \times hr}$$

st = standard, s = sample, PH = peak height, ATT = attenuation, wt = weight of tissue in g, vol = volume of container (ℓ).

Fifteen fruits were harvested at maturity from each treated limb and the weight, length (L) diameter (D) and seed number were determined for each fruit.

Experimental procedure, 1981. The experiment was repeated in 1981 using the following treatments: wetting agent only; AVG at 100 or 200 ppm; ethephon at 50 or 100 ppm; and AVG at 200 ppm plus ethephon at 100 ppm. Sprays were applied at full bloom (May 7, 8, and 13 for 'McIntosh', 'Delicious', and 'Golden Delicious', respectively, to branch units of the same 3 cultivars using one branch per treatment on each of 3 replicate trees, and fruit set, size and ethylene evolution were determined as in 1980. Frost in April killed 23% of the 'McIntosh', 16% of the 'Delicious' and 2% of the 'Golden Delicious' flowers. Damage was confined mainly to king flowers. Therefore set was recorded as fruits per 100 flowers, rather than per 100 clusters.

Average orchard temperatures during sampling for C_2H_4 measurement in 1980 and 1981 are shown in Table 1.

Results

Effects on fruit set and characteristics, 1980. Initial set on control limbs was 104, 61, and 53 and final set 33, 35 and 26 fruits per 100 flower clusters for 'McIntosh', 'Red Prince Delicious', and 'Golden Delicious', respectively, in 1980 (Table 2). Both initial and final set in 'McIntosh' were significantly higher than in either 'Golden Delicious' or 'Delicious'. 'Delicious' bore significantly less fruits per cm limb circumference than 'McIntosh' or 'Golden Delicious' but fruit retention was not affected. AVG at 200 ppm increased both initial and final set significantly in all three cultivars, but the effects of AVG at 100 ppm were significant only in 'McIntosh' (Table 2). Similarly, only in 'McIntosh' was fruits per cm limb circumference significantly increased by 200 ppm AVG. Although AVG at both concentrations appeared to increase percent fruit retention through the "June drop" in 'McIntosh' the difference was not statistically significant nor was an effect apparent in the other 2 cultivars.

At harvest time, fruits on limbs treated with 200 ppm AVG were significantly smaller than the controls in all cultivars, but the effects of 100 ppm AVG were statistically

Table 1. Mean of maximum and minimum temperatures (°C) during sampling for C_2H_4 measurement from apple flowers and young fruits at the Horticultural Research Center, East Lansing, MI 1980-81.

Days after full bloom	Cultivar					
	McIntosh		Delicious		Golden Delicious	
	1980	1981	1980	1981	1980	1981
0	11.7	12.2	9.4	7.8	13.3	2.8
1	8.9	3.9	11.7	12.8	13.9	8.3
2	9.4	7.8	12.8	13.9	15.6	10.6
3	11.7	12.2	13.3	3.9	16.7	7.8
4	12.8	13.9	13.9	2.8	18.9	6.7
5	13.3	3.9	15.6	8.3	21.1	13.3
6	13.9	2.8	16.7	10.6	20.0	7.8
7	15.6	8.3	18.9	7.8	14.4	8.3
8	16.7	10.6	21.1	6.7	12.2	10.0
9	18.9	7.8	20.0	13.3	17.8	12.8
10	21.1	6.7	14.4	7.8	21.1	17.2

Table 2. Effects of AVG and ethephon on fruit set, fruit retention, fruit per cm limb circumference and fruit characteristics at harvest of apple, E. Lansing, MI 1980.

Treatment (ppm)	Initial set[z] 6/13-15	Final set[z] 6/26-28	Fruits/cm limb circum. 6/26-28	% Fruit retention	fruit wt. (g)	L/D ratio	Seeds/ fruit
			'McIntosh'				
Check	104 c[y]	33 b	1.5 b	32 a	147 a	.79 a	6.8 b
AVG (100)	191 ab	96 a	3.8 ab	50 a	127 b	.77 a	8.3 a
AVG (200)	206 a	118 a	4.9 a	58 a	110 c	.84 a	7.5 ab
Ethephon (40)	139 bc	60 b	3.2 ab	43 a	151 a	.80 a	7.5 ab
Ethephon (80)	112 c	39 b	2.2 b	35 a	140 a	.80 a	7.3 b
Var. Mean	150 m[y]	69 m	3.1 m	46 m	----	---	---
			'Red Prince Delicious'				
Check	61 b	35 b	1.7 a	58 a	155 a	.91 a	6.3 a
AVG (100)	86 ab	44 ab	2.4 a	51 a	151 a	.92 a	6.8 a
AVG (200)	105 a	63 a	3.1 a	60 a	119 b	.93 a	5.6 a
Ethephon (40)	59 b	41 b	1.7 a	69 a	169 a	.91 a	7.6 a
Ethephon (80)	52 b	26 b	1.3 a	49 a	167 a	.91 a	7.1 a
Var. Mean	73 n	42 n	2.0 n	63 m	---	---	---
			'Golden Delicious'				
Check	53 b	26 b	2.7 a	49 a	154 ab	.91 a	5.6 a
AVG (100)	71 b	33 b	3.1 a	47 a	149 b	.86 a	5.1 a

Table 2. Continued.

Treatment (ppm)	Initial set[z] 6/13-15	Final set[z] 6/26-28	Fruits/cm limb circum. 6/26-28	% Fruit retention	fruit wt. (g)	L/D ratio	Seeds/ fruit
			'Golden Delicious'-Continued				
AVG (200)	118 a	58 a	4.1 a	49 a	128 c	.90 a	4.5 a
Ethephon (40)	43 b	24 b	2.5 a	58 a	163 ab	.89 a	5.1 a
Ethephon (80)	53 b	29 b	2.9 a	56 a	170 a	.91 a	4.9 a
Var. Mean	67 n	34 n	3.1 m	53 m	---	---	---
			Treatment Means				
Check	73 c	31 c	2.0 c	48 a	---	---	---
AVG (100)	116 b	58 b	3.1 ab	51 a	---	---	---
AVG (200)	143 a	80 a	4.0 a	65 a	---	---	---
Ethephon (40)	80 c	42 c	2.4 bc	57 a	---	---	---
Ethephon (80)	72 c	31 c	2.1 bc	50 a	---	---	---

[z]Fruits per 100 flower clusters.

[y]Mean separation within columns, cultivars and sets by DMRT, 5% level.

significant only in 'McIntosh' (Table 2). AVG had no significant effect on either L/D ratio or seed number except in 'McIntosh'; in this cultivar 100 ppm AVG significantly increased seed number per fruit, although 200 ppm did not (Table 2). Ethephon had no significant effect on any of the parameters measured.

When data were pooled for all cultivars the effects of AVG on both initial and final set were highly significant at both concentrations, and the effect of 200 ppm was significantly greater than the effect of 100 ppm (Table 2). Both AVG treatments also increased the number of fruits per cm limb circumference. Effects of ethephon were again non-significant.

Effects on ethylene evolution, 1980. AVG generally reduced ethylene evolution from flowers excised within 5 days of application (Table 3), but the differences were statistically significant in only one case ('Golden Delicious', 5 days after treatment). Little effect was evident at any time in 'McIntosh'. The burst of ethylene evolution from control 'McIntosh' flowers at 5 days was unexpected; it was not associated with high orchard temperature prior to excision (Table 1). Values for replicate samples were 48.5, 15.9, 8.9, 14.1 nℓ per g per hr. Ignoring the highest value, the mean for the remaining 3 samples is 13.0, a more reasonable number in view of other treatment data.

Ethephon at 80 ppm significantly increased ethylene

Table 3. Effects of AVG and ethephon on ethylene evolution from apple flowers and young fruits 1 to 10 days after treatment, E. Lansing, MI, 1980.

Treatment (ppm)	Ethylene production (nℓ/g f.w./hr)				
	1 day	2 days	3 days	5 days	10 days
			McIntosh		
Check	4.8 c[z]	3.6 bc	8.6 b	21.9 a	1.4 a
AVG, (100)	5.5 c	1.7 c	6.2 b	6.7 a	0.7 a
AVG, (200)	4.8 c	4.0 bc	5.3 b	8.0 a	1.3 a
Ethephon (40)	18.4 b	8.8 ab	12.4 b	19.0 a	1.5 a
Ethephon (80)	26.2 a	13.7 a	22.2 a	18.1 a	2.5 a
			Red Prince Delicious		
Check	6.4 abc	4.0 ab	8.0 a	6.2 a	3.9 a
AVG, (100)	1.2 c	2.1 bc	5.9 a	5.8 a	4.2 a
AVG, (200)	1.2 c	1.5 c	3.5 a	6.0 a	2.0 a
Ethephon (40)	13.0 a	3.4 abc	9.1 a	7.4 a	9.5 a
Ethephon (80)	11.2 ab	4.4 a	10.3 a	7.8 a	4.4 a
			Golden Delicious		
Check	5.2 b	6.0 bc	6.9 c	4.8 b	1.7 a
AVG (100)	2.6 b	3.1 c	4.1 c	0.9 c	1.2 a
AVG (200)	3.6 b	5.3 bc	3.5 c	0.8 c	0.7 a
Ethephon (40)	17.4 a	12.6 ab	13.1 b	10.8 a	2.5 a
Ethephon (80)	18.1 a	24.8 a	20.6 a	10.0 a	3.2 a

[z]Mean separation within columns and cultivars by DMRT, 5% level.

evolution in 'Golden Delicious' and 'McIntosh' flowers collected within 3 days of treatment (Table 3); 40 ppm was usually less effective. Effects of the higher concentration were still significant in 'Golden Delicious' at 5 days, but not at 10 days. Although both concentrations of ethephon approximately doubled ethylene evolution from 'Delicious' flowers collected 1 day after treatment, differences were not statistically significant, and values fell to control levels within 2 days. No consistent cultivar differences in ethylene evolution were evident in control or AVG-treated flowers, but 'Delicious' flowers treated with 80 ppm ethephon evolved significantly less ethylene than did similarly treated flowers of the other cultivars, resulting in a significant cultivar and treatment interaction (Table 4).

Effects on fruit set and characteristics, 1981. Initial set was 20, 26, and 34 and final set 13, 16, and 9 percent for control flowers of 'McIntosh', 'Delicious' and 'Golden Delicious', respectively (Table 5). Although fruit set was consistently higher following treatment with 200 ppm AVG, differences were significant only in 'Delicious' and 'Golden Delicious' and then only for initial set. Only in 'Golden Delicious' did AVG increase fruit load significantly. However, when data were pooled for the 3 cultivars, the effects of 200 ppm AVG were significant at the 1% level

Table 4. Effects of AVG and ethephon on mean ethylene production (nl/g f.w./hr) by apple flowers during three days following treatment. E. Lansing, MI 1980.

	Treatment (ppm)					
Cultivar	Control	AVG		Ethephon		Mean
		100	200	40	80	
McIntosh	5.6 cd[z]	4.5 cd	4.7 cd	13.2 b	20.7 a	9.8 v
Red Prince Delicious	6.2 cd	3.1 d	2.1 d	8.5 c	8.6 c	5.7 v
Golden Delicious	6.1 cd	3.3 d	4.1 cd	14.4 b	21.1 a	9.8 v
Mean	6.0 n	3.6 n	3.6 n	12.0 m	16.8 l	

[z]separations between cultivar means (v), treatment means (n, m, l), and cultivar x treatment means (a, b, c, d) by DMRT, 5% level. Cultivar x treatment interaction significant at 1%.

Table 5. Effects of AVG and ethephon on fruit set, fruit retention, fruits per cm limb circumference and fruit characteristics at harvest of apple, E. Lansing, MI 1981.

Treatment (ppm)	Initial set[z] 5/26-6/2	Final set 6/16-17	Fruit/cm Limb circum. 6/16-17	% Fruit Retention	Fruit wt. (g)	L/D ratio	Seeds/ fruit
			'McIntosh'				
Check	20 a	13 a	3.3 a	71 a	143 a	.79 a	7.4 a
AVG (100)	23 a	13 a	2.2 a	59 a	125 b	.80 a	7.2 a
AVG (200)	32 a	21 a	3.7 a	62 a	117 b	.79 a	6.5 a
Ethephon (50)	25 a	12 a	2.1 a	53 a	144 a	.79 a	7.7 a
Ethephon (100)	20 a	10 a	1.5 a	54 a	151 a	.80 a	7.4 a
AVG (200) + Ethephon (100)	24 a	13 a	2.6 a	61 a	116 b	.81 a	6.8 a
Var. Mean	24 n	14 m	2.6 n	60 m	-----	---	---
			'Red Prince Delicious'				
Check	26 b	16 a	3.3 a	58 a	148 ab	.92 a	4.1 a
AVG (100)	33 ab	21 a	4.7 a	65 a	136 bc	.96 a	4.5 a
AVG (200)	47 a	26 a	6.9 a	60 a	119 d	.93 a	4.1 a
Ethephon (50)	21 b	15 a	2.5 a	74 a	160 a	.92 a	4.9 a
Ethephon (100)	20 b	15 a	3.1 a	75 a	158 a	.-9 a	4.8 a
AVG (200) + Ethephon (100)	30 b	18 a	3.9 a	65 a	129 cd	.99 a	4.3 a
Var. Mean	29 mn	19 m	4.1 n	66 m	---	---	---

Table 5. Continued.

Treatment (ppm)	Initial set[z] 5/26-6/2	Final set 6/16-17	Fruit/cm Limb circum. 6/16-17	% Fruit retention	Fruit wt. (g)	L/D ratio	Seeds/ fruit
			'Golden Delicious'				
Check	34 b	9 a	4.8 b	27 a	155 a	.95 a	8.3 a
AVG (100)	46 b	13 a	8.5 a	28 a	131 a	.95 a	7.5 bc
AVG (200)	57 a	17 a	9.0 a	30 a	109 a	.95 a	6.9 c
Ethephon (50)	37 b	9 a	6.2 ab	25 a	153 a	.93 a	7.9 ab
Ethephon (100)	39 b	9 a	4.6 b	23 a	160 a	.91 b	7.5 bc
AVG (200) + Ethephon (100)	49 ab	12 a	7.1 ab	26 a	130 a	.95 a	6.1 d
Var. Mean	44 m	12 m	6.7 m	26 n	-----	.95 a	6.1 d
			Treatment Means				
Check	27 b	13 b	3.8 bc	52 a	----	---	---
AVG (100)	34 b	16 ab	5.1 ab	51 a	----	---	---
AVG (200)	45 a	21 a	6.5 a	49 a	----	---	---
Ethephon (50)	27 b	12 b	3.6 bc	51 a	----	---	---
Ethephon (100)	26 b	12 b	3.1 c	51 a	----	---	---
AVG (200) + Ethephon (100)	34 b	14 b	4.6 bc	50 a	----	---	---

[z]Fruits per 100 flowers.

[y]Mean separation within columns, cultivars, and sets by DMRT, 5% level.

for both initial and final set, as well as for fruits per cm. limb circumference. The lower concentration did not have a significant effect. Effects on fruit retention through the "June drop" were again not significant.

AVG reduced fruit weight in all cases whether used alone or with ethephon; the reduction was statistically significant at both concentrations in 'McIntosh', neither concentration in 'Golden Delicious' and at 200 ppm only in 'Delicious'. When AVG was applied with ethephon, differences in fruit weight were significant in 'McIntosh' and 'Delicious', but not in 'Golden Delicious'. All AVG treatments significantly reduced seed number in 'Golden Delicious' (Table 5), but L/D ratios were not affected in any cultivar.

Ethephon had no significant effect on fruit set, retention or characteristics when used alone at either 50 or 100 ppm, except for a reduction in seed number in 'Golden Delicious' at the higher concentration. At 100 ppm ethephon prevented a significant fruit setting response to 200 ppm AVG when the two chemicals were applied together.

Initial set of 'Golden Delicious' was significantly greater than that of 'McIntosh', but not of 'Delicious', but cultivar differences in final set were non-significant. The varietal mean for fruit per cm. limb circumference in 'Golden Delicious' was significantly greater than those of the other cultivars, mainly because of greater flower

density and less frost damage; however, fruit retention was significantly lower (Table 5).

Effects on ethylene evolution, 1981. Ethylene evolution was generally lower in AVG-treated flowers of all three cultivars, but the effects were statistically significant in only one cultivar at one sampling date ('Golden Delicious', 5 days after treatment) (Table 6). Ethephon significantly increased ethylene evolution in all three cultivars, although response varied with time of sampling. Ethylene evolution was 2- to 10-fold as high in ethephon-treated flowers as in controls during the 3 days following treatment; after 10 days the difference was significant only in 'Golden Delicious' flowers treated with 100 ppm. AVG treatment had no significant effect on response to ethephon although ethylene levels were generally lower when AVG was used. Ethephon-treated 'Delicious' flowers again evolved significantly less ethylene than did similarly treated 'McIntosh' flowers, and 'McIntosh' significantly less than 'Golden Delicious' following treatment with 100 ppm ethylene, with or without AVG (Table 7). Values for control and AVG-treated flowers were not significantly affected by cultivar, confirming the results obtained in 1980. This again resulted in significant interaction between cultivar and treatment.

Table 6. Effects of AVG and ethephon on ethylene production of apple flowers and young fruits as a function of days after treatment, E. Lansing, MI, 1981.

Treatment (ppm)	Ethylene production (nℓ/g f.w./hr)				
	1 Day	2 Days	3 Days	5 Days	10 Days
			McIntosh		
Check	6.6 a[z]	2.6 c	1.4 bc	4.2 bcd	4.2 ab
AVG (100)	1.5 a	1.6 c	2.3 bc	2.7 cd	2.2 bc
AVG (200)	6.5 a	1.3 c	0.6 c	1.5 d	2.8 bc
Ethephon (50)	19.2 a	13.6 b	2.8 ab	5.5 abc	3.6 b
Ethephon (100)	17.6 a	25.8 a	4.4 a	7.9 a	5.6 a
AVG (200) + Ethephon (100)	19.0 a	20.1 ab	2.8 ab	6.6 ab	4.0 b
			Red Prince Delicious		
Check	0.9 b	1.6 bc	3.4 ab	3.4 bc	5.2 a
AVG (100)	0.5 b	0.5 c	1.7 b	2.2 c	6.8 a
AVG (200)	0.4 b	0.6 c	1.1 b	2.4 c	4.3 a
Ethephon (50)	5.0 a	3.3 ab	5.9 a	5.3 a	6.1 a
Ethephon (100)	3.9 a	4.0 a	5.1 a	4.9 ab	5.9 a
AVG (200) + Ethephon (100)	4.9 a	3.6 a	4.8 a	4.2 ab	5.3 a
			Golden Delicious		
Check	3.2 c	4.2 bc	13.8 bc	9.7 b	2.4 bc
AVG (100)	1.9 c	1.6 c	3.4 c	5.6 bc	2.0 bc
AVG (200)	1.6 c	1.4 c	3.1 c	2.1 c	1.8 c
Ethephon (50)	12.4 b	11.5 b	26.0 ab	9.5 ab	4.4 ab
Ethephon (100)	18.8 a	24.9 a	39.8 a	11.5 ab	5.2 a
AVG (200) + Ethephon (100)	14.4 ab	21.9 a	28.3 a	15.2 a	6.5 a

[z]Mean separation within columns and cultivars by DMRT, 5% level.

Table 7. Effects of AVG and ethephon on mean ethylene production (nl/g f.w./hr) by apple flowers during three days following treatment. E. Lansing, MI 1981.

Cultivar	Treatment (ppm)						
	Control	AVG		Ethephon		AVG + Ethephon	Mean
		100	200	50	100	200 + 100	
McIntosh	3.5 e[z]	1.8 e	2.77 e	11.8 cd	15.9 c	13.9 c	8.3 w
Red Prince Delicious	2.1 e	0.9 e	0.67 e	4.6 e	4.2 e	4.3 e	2.8 x
Golden Delicious	7.4 de	2.4 e	2.09 e	17.3 bc	28.8 a	22.3 b	13.4 v
Mean	4.3 n	1.7 n	1.9 n	11.2 m	16.3 l	13.5 lm	

[z]separations between cultivar means (v, w, x), treatment means (n, m, l), and cultivars x treatment mean (a, b, c, d, e) by DMRT, 5% level. Cultivar x treatment interaction significant at 1%.

Discussion

The data obtained in this study confirm previous results (Dennis, 1978; Archbold and Dennis, unpublished; Greene, 1980, Williams, 1980) that AVG increases fruit set and inhibits ethylene biosynthesis in apple flowers. However, its fruit setting effect does not appear to be dependent upon inhibition of ethylene synthesis as proposed by Greene (1980) and Williams (1980). They suggested that apple fruit set is limited by the rate of ethylene synthesis in the flower. If this were true, reducing the rate of ethylene production should promote fruit set and increasing the rate should reduce set, i.e., fruit set should be negatively correlated with ethylene production.

My data relating fruit set to ethylene evolution are summarized in Figure 1. High levels of ethylene evolution were not induced in 'Delicious' by treating with ethephon. However, in 'McIntosh' and 'Golden Delicious' high levels of ethylene did not reduce set. Furthermore, although AVG concentration had little effect upon ethylene evolution, set almost invariably increased as the concentration of AVG increased from 100 to 200 ppm. Correlation coefficients for initial fruit set vs. ethylene evolution were not statistically significant for any cultivar in 1980 or 1981 (Table 8). However, the r values for 'Delicious' were high and

Figure 1. Relationship between mean ethylene evolution from flowers the first three days after treatment and initial fruit set of apple.

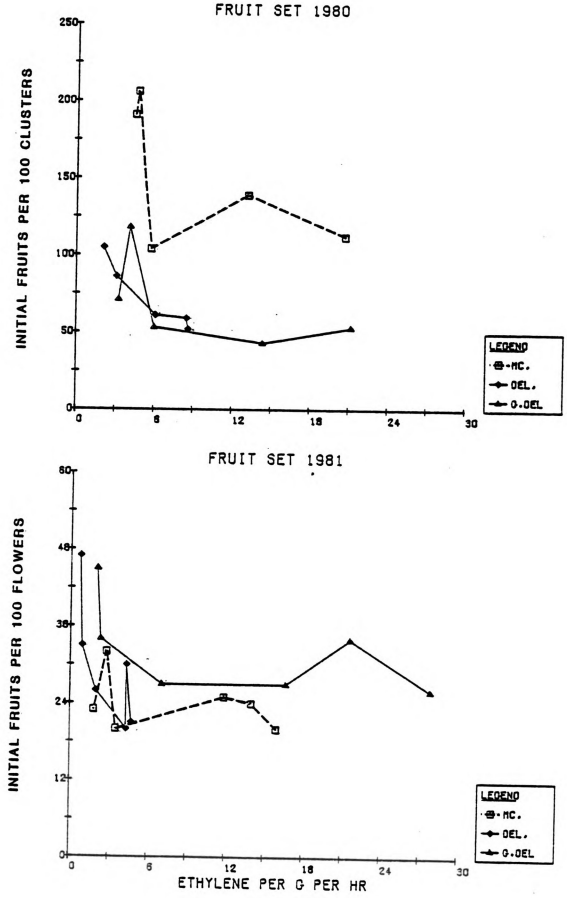
FRUIT SET 1980
INITIAL FRUITS PER 100 CLUSTERS
250
200
150
100
50
0
0
6
12
18
24
30
LEGEND
MC.
DEL.
G.DEL
FRUIT SET 1981
INITIAL FRUITS PER 100 FLOWERS
60
48
36
24
12
0
0
6
12
18
24
30
ETHYLENE PER G PER HR
LEGEND
MC.
DEL.
G.DEL

Figure 1

Table 8. Relationship between initial fruit set of apple and mean ethylene evolution from flowers during 3 days following chemical treatment.

Cultivar	Correlation coefficient[z] 1980	1981
McIntosh	-0.38	-0.33
Delicious	-0.77	-0.76
G. Delicious	-0.57	-0.58

[z]No values significant at 5% level. Five (1980) or 6 (1981) pairs of observations per cultivar.

might have been significant with more observations. Thus there appears to be a negative correlation between fruit set and ethylene evolution in 'Delicious' but not in 'McIntosh' or 'Golden Delicious'. Therefore the hypothesis that ethylene level controls fruit set may still be true for 'Delicious'.

Untreated 'Delicious' flowers could produce more ethylene than do 'McIntosh' and 'Golden Delicious' flowers and therefore set comparatively poorly. However, the data (Tables 4 and 7) indicate no consistent cultivar differences in ethylene production in untreated flowers in 1980, and a lower (difference non-significant at 5%) production in 'Delicious' in 1981. Therefore this hypothesis is not valid.

There remains the possibility that 'Delicious' flowers are more sensitive to ethylene levels. If this were true, one should expect lower fruit set in 'Delicious' than in other cultivars at the same endogenous level of ethylene. Although the ratio of fruit set to ethylene production was higher for 'McIntosh' than for 'Delicious' in 1980, it was similar in 1981 (Figure 1). Likewise, the ratio was higher for 'Golden Delicious' in 1981, but similar in 1980. Therefore, this hypothesis too does not appear to be valid.

Low concentrations (40 to 100 ppm) of ethephon markedly increased ethylene evolution without affecting set appreciably. Higher concentrations (200 to 1000 ppm) of

ethephon probably would have reduced fruit set (see Edgerton and Greenhalgh, 1969).

I conclude that the rates of ethylene production measured in this study have little or no effect on fruit set of apple.

AVG had no significant effect on set when applied with ethephon, nor did it reduce the effect of ethephon on ethylene evolution from the flowers. The combined effects of AVG and ethephon on fruit set are difficult to explain. If the effect of AVG is not mediated by ethylene, and if ethephon alone does not decrease set, application of AVG with or without ethephon should increase set. However, application of ethephon at 100 ppm eliminated the effect of 200 ppm AVG (Table 5), at least in 'McIntosh' and 'Delicious'. Perhaps a high level of ethylene within the tissue blocks the promotive action of AVG without directly reducing set. This possibility should be explored in other systems.

If the petals were the major source of ethylene, the ethylene production measured in this study would not have been that which is crucial in regulating set. However, petal removal had no consistent effect upon rate of ethylene evolution (Table 9). Therefore, most of the ethylene measured was probably evolved from other flower tissues. Nichols (1977) observed that approximately 40 to 50% of the ethylene evolved by carnation flowers could be accounted for by the styles and most of the remainder by

Table 9. Effect of petal removal on ethylene production by apple flowers, 1981.

	Ethylene production (nℓ per g per hr)[z]			
	1 day AFB[y]		2 days AFB	
Cultivar Petals:	Intact	Removed	Intact	Removed
McIntosh	6.62[x]	0.91	2.57	3.57
Delicious	0.88	0.82	1.61	1.02
Golden Delicious	3.20	3.40	4.19	4.87

[z]Treatment differences not significant, 5% level.

[y]After full bloom.

[x]Means for 1 limb on each of 3 trees in RCB.

the petals. Because the styles contributed less than 4% of the fresh weight of the flowers, they were considered to be the most active centers of ethylene production. Ethylene production by the style, ovary tissue or ovules might be better correlated with fruit set than production by the entire flower.

Cultivar differences were evident in response to ethephon treatment, treated flowers of 'McIntosh' and 'Golden Delicious' producing much more ethylene than those of 'Red Prince Delicious'. Tissues with different acidities might be expected to show different capacities for ethylene evolution (Warner and Leopold, 1969). Tissues of 'Delicious' flowers may have a lower pH than those of 'McIntosh' and 'Golden Delicious', resulting in less breakdown of ethephon and therefore slower release of C_2H_4.

Breakdown of ethephon is highly dependent on temperature (Olien and Bukovac, 1978; Amchem Products, Inc., 1969). In this study variation in ethylene production by flowers treated with ethephon did not appear to be an effect of temperature differences (Table 6).

Differences in ethylene evolution do not appear to be responsible for differences in initial fruit set. and the effects of AVG in increasing set apparently are independent of its effects on ethylene synthesis. The mechanism of action of AVG in stimulating fruit set remains to be determined. The chemical could increase ovule longevity and this possibility is explored in a subsequent study.

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SECTION II

RELATIONSHIP BETWEEN ENDOGENOUS ETHYLENE EVOLUTION AND APPLE FRUIT ABSCISSION DURING "JUNE" DROP

Abstract. Sprays of aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, silver thiosulfate (STS), an inhibitor of ethylene action, and (2-chloroethyl) phosphonic acid (ethephon), an ethylene-generating compound, were applied to branch units of 'McIntosh', 'Red Prince Delicious', and 'Golden Delicious' apple (Malus domestica Borkh.) trees 18 or 21 days after full bloom. The bark on additional limbs was scored with a knife. AVG (200 ppm) had no significant effect on ethylene evolution in any of the cultivars, but significantly reduced fruit retention in 'McIntosh' in 1980. Scoring and STS treatment affected neither ethylene production nor abscission. Ethephon (200 ppm) significantly increased fruit abscission in all 3 cultivars, but 100 ppm was effective only in 'McIntosh' and 'Golden Delicious'.

Ethylene evolution was measured in two populations of fruits differing in diameter. Small fruits generally produced more ethylene per unit weight and their abscission potential was higher than large fruits sampled at the same time. However, ethylene production of untreated fruits appeared to be a function of fruit size rather than of abscission potential per se. The data suggest that ethylene production is not the primary factor controlling abscission of apple fruits during the "June" drop.

Two abscission periods are usually recognized in apple trees, one termed "first drop" immediately following bloom and the other "June" drop approximately 2 to 3 weeks after bloom (Gourley and Howlett, 1957; Teskey and Shoemaker, 1972; Childers, 1969). Several factors have been suggested as being responsible for the second drop, including low seed number and competition between fruits for food materials (Gourley and Howlett, 1957; Teskey and Shoemaker, 1972). Heinicke (1917) reported that apples which fell from the tree contained fewer developing seeds than those which remained on the tree. However, the mechanism of fruit abscission is still not well understood.

Since the discovery of ethylene as a natural plant hormone and its action in fruit abscission, several investigators have suggested that it plays a role in "June drop" (Dennis, 1970). Blanpied (1972) found that during the June drop the fruit pedicel of 'McIntosh' and 'Delicious' apple contained 3- to 10-fold more ethylene per unit weight than did fruit flesh tissues and that tissues of abscising fruits pedicel and flesh tissues did not consistently contain more ethylene than similar tissue of adhering fruits.

Certain chemicals are effective in either stimulating or inhibiting the "June" drop in apple. Synthetic auxins such as naphthaleneacetic acid (NAA) and its derivatives have been used as thinning agents in apple for many years. The mechanism of action of NAA is still not well understood,

but one hypothesis is that application of NAA stimulates ethylene synthesis and that the ethylene produced induces abscission of immature fruits (Dennis, 1970; Schneider, 1975; Walsh, et al., 1979). Several investigators have reported that NAA does indeed stimulate ethylene evolution in apple fruits. Schneider (1975) found that spraying with NAA (25 ppm) 4 days after petal fall stimulated both fruit abscission and ethylene evolution in leaves, fruits and pedicels of 'Golden Delicious', 'Staymared' and 'Red Rome' apple sampled 24 hours and 48 hours after spraying. He suggested that NAA-induced ethylene evolution caused fruit abscission. Walsh, et al. (1979) sprayed branches of 'Golden Delicious' and 'Northern Spy' apple with NAA (15 ppm) two weeks after petal fall. One day after application ethylene evolution from 'Golden Delicious' spurs was 5 times greater than that from controls, and the chemical significantly thinned both cultivars. Williams (1980b) applied NAA at 5 and 10 ppm to 'Delicious' apple two weeks after full bloom. NAA at both concentrations significantly increased ethylene evolution 24 hrs. after application and reduced fruit set.

Ethephon ((2-chloroethyl)phosphonic acid), which releases ethylene within the tissues, also can be used as a thinning agent. Its effectiveness on apple fruits depends on the time of application and the cultivar. Walsh, et al. (1979) successfully thinned 'Golden Delicious' and 'Northern

Spy' by applying 200 ppm 2 weeks after full bloom. When applied 10 days after full bloom 50 ppm ethephon did not thin 'McIntosh' fruits, but 250 and 500 ppm were effective; 75 and 250 ppm applied 28 and 44 days after full bloom had no significant effect (Edgerton and Greenhalgh, 1966). However, concentrations of 200 to 400 ppm applied 35 and 42 days after full bloom eliminated all fruits on 'Jonathan', 'Richared Delicious' and 'Gravenstein' trees in Australia (Veinbrants, 1979). Walsh, et al. (1979) sprayed 'Golden Delicious' and 'Northern Spy' apple fruits with 200 ppm ethephon two weeks after petal fall. Ethylene evolution from spurs of 'Golden Delicious' was 7 times higher than in control spurs and the chemical significantly thinned both cultivars.

Williams (1980a) applied 1000 ppm of aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, to 'Delicious' and 'Golden Delicious' apple 2 weeks after full bloom. The treatment complete by inhibited "June" drop and Williams suggested that the effect on drop might be a result of reduced ethylene synthesis. AVG (400 ppm) counteracted the effects of NAA (10 ppm) on both ethylene evolution and fruit abscission (Williams 1980b). Rates of ethylene evolution were 4.4, 6.7, 1.8, and 1.5 µℓ per g per hour for control, NAA alone, AVG alone and AVG + NAA, respectively, and fruit set values (fruits per 100 clusters) were 89, 49, 116, and 80, respectively. Note that fruit set in the last

two treatments differed markedly, yet ethylene evolution was identical. AVG (200 ppm) applied to 'Golden Delicious' fruitlets prior to treatment with NAA (58 ppm) did not reduce the effect of the latter on ethylene synthesis (Ebert 1980).

Silver nitrate and silver thiosulfate inhibit ethylene action rather than its biosynthesis (Burg and Burg, 1967; Reid, et al., 1980; Miranda, 1981). Spraying pea seedlings with silver nitrate effectively blocks the ability of exogenous ethylene to induce the classical "triple" response --- growth retardation, stem swelling and horizontal growth. Treatment with $AgNO_3$ blocks leaf abscission in cotton (Beyer, 1976) and delays senescence as well as counteracting the effects of ethephon in excised carnation flowers (Halevy and Kofranek, 1977). In banana fruit slices, $AgNO_3$ significantly reduced ethylene production (Saltveit, et al., 1978). However, sweet potato (Walker, et al., 1979) and apple (Greene, 1980) tissues treated with Ag^+ produced more ethylene than the control.

Several reports indicate that ringing or scoring limbs before or two weeks after full bloom can also reduce the severity of the "June drop" in apple (Murneek, 1937; Griggs and Schrader, 1941; Batjer, 1962; Dennis and Edgerton, 1965) possibly by preventing translocation of reserve carbohydrates from the treated branch. Some evidence indicates that ringing alters endogenous ethylene levels

(Singh and Weaver, 1976). Girdling of grape canes promoted ethylene volution from the fruit at all stages of berry development (Singh and Weaver, 1976). Weaver, et al. (1972) showed that ethephon moved from leaf to the shoot tip and suggested that the compound was translocated from source to sink. Hale and Weaver (1962) had previously shown that growing berries attract assimilates and ethylene from the foliage.

The purpose of this study was to evaluate the role of endogenous ethylene production in controlling the "June drop" of 'Delicious', 'Golden Delicious' and 'McIntosh' apple fruits. Both stimulators and inhibitors of ethylene evolution were used and their effects upon abscission vs. ethephon evolution were compared.

Materials and Methods

In 1980 mature 'Red Prince Delicious', 'Golden Delicious', and 'McIntosh' apple trees were used and 6 uniform limbs were selected on each of 3 trees per cultivar. Eighteen days after full bloom (FB) one of the following treatments was applied to one branch on each tree: double scoring through the bark with a knife with scores 2 cm apart; AVG at 50 or 200 ppm; ethephon at 100 or 200 ppm. One hundred fruits on each limb were counted for evaluation of fruit retention. Fifty control fruits of 'Delicious',

'McIntosh' and 'Golden Delicious' and 50 'Golden Delicious' fruits treated with 200 ppm AVG and ethephon were identified with numbered tags on each tree, and fruit number and diameter were recorded at intervals. Five small and five large fruits in the population present on a given date were harvested from each tagged limb 1, 3, 6, 9 and 12 days after application. These small and large fruits were held in separate sealed 135 ml containers in the dark at 21°C and CO_2 was absorbed by placing a filter paper wick moistened with 40% KOH in each container. The jars were ventilated after 4 hours and ethylene accumulation was monitored by removing a one ml gas sample through a serum cap after an additional 4 hour period. Ethylene was determined using a gas chromatograph (Varian Aerograph Series 1700 or 1400), equipped with a flame ionization detector. A column (45 x 0.32 cm) of 60 to 80 mesh Al_2O_3 was used at 60° or 80°C. The amount of ethylene evolved per g tissue per hour was calculated by the following formula:

$$C_2H_4{}_s \ (\mu\ell\ g^{-1}.hr^{-1}) = \frac{C_2H_4{}_{st}\ (ppm) \times PH_s \times vol(\ell)}{ATT_{st} \times PH_{st} \times wt_s \times hr}$$

st = standard; s = sample; PH = peak height; ATT = attenuation; wt = weight in g, vol = volume of container (ℓ).

In 1981 treatments were applied in a similar experiment using 3 trees each of 'McIntosh' and 'Red Prince Delicious'. The following treatments were applied three weeks after full bloom; AVG, 200 ppm; ethephon, 100 or 200 ppm; AVG, 200 ppm, plus ethephon, 200 ppm; silver thiosulfate (STS), 100 ppm. The STS solution was prepared by adding 1 M $AgNO_3$ to an equal volume of 4 M $Na_2S_2O_3 \cdot 5H_2O$ with rapid stirring. Diameters of fruits receiving no treatment, 200 ppm AVG or 200 ppm ethephon were measured to the nearest mm at 3 day intervals for 18 days beginning on the day of treatment. Ethylene production by large and small fruits was measured as in 1980. Orchard temperatures during the sampling period were recorded for both years (Table 1).

Results

1980. Double scoring did not affect fruit retention significantly in any of the 3 cultivars (Table 2), although fruit number was reduced in 'McIntosh', and increased in 'Delicious'. Because interaction between treatment and fruit size was non-significant, only main effects on ethylene evolution are presented (Tables 3 and 4). Although ethylene production was generally lower in fruits from scored limbs than in control fruits of 'McIntosh' and 'Golden Delicious', the reduction was not significant

Table 1. Mean of maximum and minimum temperatures (°C) during time of sample collection for ethylene determination in apple fruits at the Horticultural Research Center, East Lansing, MI.

Days after treatment	McIntosh		Red Prince Delicious		Golden Delicious
	1980	1981	1980	1981	1980
1	15.0	16.1	15.0	12.8	10.6
2	17.2	19.4	10.0	12.8	7.8
3	17.2	12.8	10.6	15.6	12.2
4	18.9	12.8	7.8	18.9	17.2
5	15.0	15.6	12.2	20.0	20.0
6	10.0	18.9	17.2	16.7	19.4
7	10.6	20.0	20.0	21.7	11.7
8	7.8	16.7	19.4	16.7	11.7
9	12.2	21.7	11.7	21.1	15.6
10	17.2	16.7	11.7	19.4	16.7
11	20.0	21.1	15.6	17.8	15.0
12	19.4	19.4	16.7	16.7	15.0

Table 2. Effects of AVG, ethephon and double scoring on fruit retention and fruit diameter of apple 1980. Sprays applied June 3 ('McIntosh'), 8 ('Delicious') or 9 ('Golden Delicious').

Observation	Treatment					
			AVG (ppm)		Ethephon (ppm)	
	None	Scoring	50	200	100	200
			'McIntosh'[z]			
Fruit retention (%) 6/20	57.0 a[y]	49.1 ab	16.9 c	30.5 bc	11.3 c	9.6 c
Fruit diameter (mm) 7/29	53.7 a	55.0 a	53.0 a	52.3 a	52.3 a	52.0 a
			'Red Prince Delicious'[z]			
Fruit retention (%) 6/21	50.6 bc	68.0 ab	63.7 ab	72.5 a	78.1 a	32.0 c
Fruit diameter (mm) 7/29	49.3 a	50.0 a	46.3 b	49.3 a	51.0 a	51.0 a
			'Golden Delicious'[z]			
Fruit retention (%) 6/21	33.9 ab	39.3 a	39.0 a	44.4 a	25.1 b	26.9 b
Fruit diameter (mm) 7/30	50.0 a	52.0 a	50.3 a	48.0 a	48.7 a	48.7 a

[z]Mean initial number of fruits 50 to 79 (McIntosh), 30 to 49 (Red Prince Delicious) and 41 to 60 (Golden Delicious).

[y]Mean separation within cultivars and observations by DMRT, 5% level.

Table 3. Effects of aminoethoxyvinylglycine (AVG) ethephon and double scoring on ethylene evolution (nℓ/g/hr) from 'McIntosh' apple fruits prior to "June" drop 1980. Treatments applied June 3.

Treatment (ppm)	Days after treatment					
	1	3	6	12	1+3	1+3+6
None	2.92 bc[z]	5.24 b	4.14 a	1.96 bc	4.09 bc	4.1 bc
Scoring	0.36 c	4.29 b	3.57 a	1.37 c	2.32 bc	2.74 c
AVG (50)	0.72 c	4.47 b	5.52 a	1.83 bc	2.59 bc	3.57 bc
AVG (200)	0.27 c	0.85 c	3.72 a	1.33 c	0.55 c	1.61 c
Ethephon (100)	6.18 b	12.18 a	5.10 a	3.13 ab	9.18 ab	7.82 ab
Ethephon (200)	16.15 a	13.83 a	6.09 a	3.61 a	14.99 a	12.03 a
Mean for						
Large fruits	2.96 m	4.67 m	4.10 ℓ	1.57 m	3.82 m	3.91 m
Small fruits	5.91 ℓ	8.95 ℓ	5.28 ℓ	2.84 ℓ	7.43 ℓ	6.71 ℓ

[z]Mean separation within columns and sizes by DMRT, 5% level.

Table 4. Effects of aminoethoxyvinylglycine (AVG), ethephon and double scoring on ethylene evolution (nℓ/g/hr) from 'Red Prince Delicious' and 'Golden Delicious' apple fruits prior to "June" drop 1980. Treatments applied June 5 ('Delicious') or 9 ('Golden Delicious').

Treatment (ppm)	Days after treatment					
	1	3	9	12	1+3	1+3+9
			'Red Prince Delicious'			
None	11.26 b	8.49 b	2.05 c	0.45 c	9.87 c	7.27 c
Scoring	11.32 b	2.42 b	2.14 c	0.77 c	6.87 c	5.30 c
AVG (50)	8.44 b	2.31 b	2.28 c	0.54 c	5.37 c	4.33 c
AVG (200)	4.65 b	1.82 b	1.73 c	0.57 c	3.37 c	2.73 c
Ethephon (100)	32.83 a	9.15 b	5.94 b	1.76 b	20.99 b	15.98 b
Ethephon (200)	38.49 a	19.85 a	10.22 a	4.52 a	29.17 a	22.85 a
Mean for						
Large fruits	12.64 m	5.20 m	3.46 ℓ	1.25 ℓ	8.92 ℓ	7.10 m
Small fruits	23.03 ℓ	9.48 ℓ	4.66 ℓ	1.61 ℓ	16.26 ℓ	12.39 ℓ
			'Golden Delicious'			
None	9.97 b	13.12 b	6.38 bc	1.76 b	11.54 bc	9.82 bc
Scoring	7.38 b	10.04 b	4.06 bc	1.53 b	8.71 bc	7.16 bc
AVG (50)	4.71 b	3.14 b	3.54 bc	1.47 b	3.93 c	3.79 cd
AVG (200)	2.12 c	3.54 b	2.14 c	1.20 b	2.83 c	2.60 d
Ethephon (200)	22.21 a	8.51 b	7.16 b	4.09 a	15.36 b	12.63 b
Ethephon (100)	22.83 a	30.97 a	13.61 a	5.43 a	26.90 a	22.47 a
Mean for						
Large fruits	11.46 ℓ	11.65 ℓ	5.67 ℓ	2.25 ℓ	11.55 ℓ	9.60 ℓ
Small fruits	11.61 ℓ	11.46 ℓ	6.52 ℓ	2.87 ℓ	11.55 ℓ	9.90 ℓ

[z]Mean separation within cultivars, columns and sizes by DMRT, 5% level.

at the 5% level.

AVG at both concentrations significantly reduced fruit retention in 'McIntosh' (Table 2). Although AVG increased retention in both 'Delicious' and 'Golden Delicious', the differences were significant only in 'Delicious' and then only at 200 ppm. Effects on fruit size were small and inconsistent. AVG at 200 ppm appeared to reduce ethylene evolution in all 3 cultivars (Tables 3 and 4), but the reduction was significant only in 'Golden Delicious' 1 day after treatment, even when means for several days were compared. At 50 ppm, AVG generally reduced ethylene evolution, but differences were non-significant.

Ethephon at both 100 and 200 ppm significantly increased fruit drop in 'McIntosh' but not in 'Delicious' or 'Golden Delicious'. Although drop was heavier on limbs of the last two cultivars which were treated with 200 ppm ethephon, the effects were non-significant (Table 2). In 'Delicious' the low concentration actually reduced drop significantly. Effects upon fruit size were small and non-significant. At the higher concentration, ethephon increased ethylene evolution from treated fruits regardless of cultivar or time of sampling except in 'McIntosh' fruits sampled 6 days after treatment (Table 3 and 4). The effects of 100 ppm were similar, but with fewer significant differences.

Small 'McIntosh' and 'Delicious' fruits evolved significantly more ethylene per g fresh weight than large

ones with few exceptions, but fruit size had no significant effect on ethylene production in 'Golden Delicious'.

1981. AVG tended to increase fruit retention in both cultivars, but the differences were not statistically significant (Table 5). Seed number, fruit size, and L/D ratio were not significantly affected in either cultivar, although 'McIntosh' fruits treated with both AVG and ethephon appeared to be smaller. Data on ethylene evolution from large and small fruits were again pooled, as interaction between treatment and fruit size was non-significant. AVG alone generally reduced ethylene production, but the effect was not significant, even when data for several sampling dates were pooled (Table 6).

Ethephon alone did not affect fruit retention significantly in either cultivar (Table 5), nor did it alter seed number, fruit weight, or L/D ratio. Ethephon at 200 ppm consistently increased ethylene evolution; effects of 100 ppm were intermediate and were significant on 3 ('McIntosh') or 4 ('Delicious') of the 5 sampling dates (Table 6).

AVG plus ethephon reduced fruit retention, but the effects were significant only in 'McIntosh' (Table 5). Treated fruits of both cultivars were smaller than controls, but effects on size and L/D ratio were non-significant. Seed number was significantly reduced in

Table 5. Effects of AVG, ethephon and silver thiosulfate (STS) on fruit abscission and fruit characteristics at harvest of 'McIntosh' and 'Red Prince Delicious' apple, 1981. Treatments applied May 28 ('McIntosh'), or 30 ('Delicious').

Treatment (ppm)	Fruit Retention (%) 6/16	No. seeds Per fruit	Fruit wt (g)	L/D ratio
		'McIntosh'[z]		
None	36 ab	6.9 a	147 a	0.78 a
AVG (200)	50 a	7.4 a	122 a	0.80 a
Ethephon (100)	29 bc	7.2 a	150 a	0.79 a
Ethephon (200)	26 bc	7.4 a	135 a	0.83 a
AVG (200) + Ethephon (200	18 c	5.7 b	137 a	0.81 a
STS	41 ab	7.0 a	143 a	0.77 a
		'Red Prince Delicious'[z]		
None	71 a	4.1 a	148 a	0.91 a
AVG (200)	88 a	4.1 a	152 a	0.89 a
Ethephon (100)	70 a	4.4 a	151 a	0.93 a
Ethephon (200)	62 a	4.8 a	155 a	0.88 a
AVG (200) + Ethephon (200)	60 a	4.8 a	133 a	0.86 a
STS (100)	74 a	4.3 a	141 a	0.92 a

[z]Mean initial fruit numbers 90 to 97 ('McIntosh') and 64 to 81 ('Delicious').

[y]Mean separation within columns and cultivars by DMRT, 5% level.

Table 6. Effects of aminoethoxyvinylglycine (AVG), ethephon and silver thiosulfate on ethylene evolution (nℓ/g/hr) from 'McIntosh' and 'Red Prince Delicious' apple fruits prior to "June" drop 1981. Treatments applied May 28 (McIntosh), or 30 (Red Prince Delicious).

Treatment (ppm)	Days After Treatment						
	1	3	6	9	12	1+3	1+3+6
				'McIntosh'			
Check	1.22 c[z]	2.03 c	0.71 c	0.62 b	0.19 c	1.62 c	1.32 c
AVG (200)	1.52 c	1.62 c	0.56 c	0.44 b	0.24 c	1.57 c	1.23 c
Ethephon (100)	8.72 bc	6.78 b	2.91 b	1.38 b	0.54 b	7.75 b	6.14 b
Ethephon (200)	19.12 a	8.73 a	4.23 a	3.55 a	0.95 a	13.92 a	10.69 a
AVG (200) + Ethephon (200)	15.68 ab	6.99 b	3.32 ab	0.93 b	0.56 b	11.34 ab	8.66 ab
STS	1.77 c	1.98 c	2.93 b	1.49 b	0.23 c	1.88 c	2.22 c
Mean for							
Small fruits	8.92 ℓ	5.66 ℓ	3.02 ℓ	1.45 ℓ	0.51 ℓ	7.29 ℓ	5.87 ℓ
Large fruits	7.09 ℓ	3.72 m	1.87 m	1.34 ℓ	0.39 m	5.40 m	4.22 m
				'Red Prince Delicious'			
Check	1.17 b	1.59 c	1.20 b	0.65 c	0.35 d	1.38 d	1.32 cd
AVG (200)	0.74 b	0.85 c	1.29 b	0.34 c	0.26 d	0.79 d	0.96 d
Ethephon (100)	5.05 ab	4.16 b	4.51 a	1.14 b	0.56 c	4.61 bc	4.57 b
Ethephon (200)	9.17 a	6.39 a	4.71 a	2.02 a	1.02 a	7.78 a	6.76 a
AVG (200) + Ethephon (200)	6.38 a	7.15 a	2.73 b	1.97 a	0.76 b	6.76 ab	5.42 ab
STS	5.14 ab	1.10 c	2.22 b	0.45 c	0.32 d	3.12 cd	2.82 c
Mean for							
Small fruits	4.68 ℓ	4.33 ℓ	3.43 ℓ	1.48 ℓ	0.59 ℓ	4.51 ℓ	4.15 ℓ
Large fruits	4.54 ℓ	2.75 m	2.13 m	0.70 m	0.50 ℓ	3.64 m	3.14 m

[z]Mean separation within cultivars, columns and sizes by DMRT, 5% level.

'McIntosh', but not in 'Delicious'. Ethylene evolution was consistently reduced in comparison with ethephon alone with one exception ('Delicious' at 3 days), differences being significant in 5 of 10 cultivar-date combinations (Table 6). However, values were significantly higher than control values in all but two cases ('McIntosh', 9 days, 'Delicious', 6 days after treatment).

Silver thiosulfate did not significantly affect fruit retention, fruit size, seed number or L/D ratio in either cultivar (Table 5), and ethylene production was affected (increased) significantly in only one case ('McIntosh', 6 days) (Table 6).

Small fruits evolved consistently more ethylene per g fresh weight than did large ones, and differences were significant in 10 of 14 comparisons (Table 6).

In the previous paper I observed that 'Delicious' apple flowers consistently evolved less ethylene following treatment with ethephon than did similarly treated 'McIntosh' or 'Golden Delicious' flowers. However, cultivar differences in the response of developing fruitlets was inconsistent. Treated 'Delicious' fruitlets evolved more ethylene in 1980, but less in 1981, than did 'McIntosh' fruitlets (Tables 3, 4, and 6).

Abscission data obtained from untreated, tagged fruits which were measured periodically in 1980 indicated that abscission potential decreased as fruit size increased

(Figure 1) as previously demonstrated by Zucconi (1975, 1978) for peach and orange fruits. In 'McIntosh', for example, fruits 9 mm or less in diameter as of June 3 had all abscised by June 15, whereas no fruits 15 mm or greater in diameter had fallen. As fruit diameter increased from 10 to 14 mm, fruit drop decreased. Data for 'Delicious' and 'Golden Delicious' fruits were parallel, but abscission potential was greater than for 'McIntosh' fruits of similar size.

To determine the relationship between ethylene evolution and abscission potential, the fruits used for ethylene determination were stored in plastic bags at 4°C for two weeks. The diameter and weight of each fruit was then measured and a curve constructed relating the two (Figure 2). This curve was used to convert the mean weights of both large and small fruits to mean diameters for each sampling data (Table 7). Data for abscission potential obtained from tagged fruits were then plotted against diameter of the fruits remaining at each sampling date (Figure 3) and the abscission potentials of large and small fruits estimated from these graphs using their mean diameters as indices (Table 7). The data indicate that small fruits generally had both a higher abscission potential (Table 7) and a higher rate of ethylene production (Table 7, Figure 4A and C) than did large fruits.

These differences in ethylene evolution could be responsible for differences in abscission potential. On

Figure 1. Effect of cultivar on relationship between fruit diameter on June 3 (McIntosh), 8 (Delicious) or 9 (Golden Delicious) and abscission during "June" drop 1980. Surviving fruits counted June 15 (McIntosh), 20 (Delicious) or 21 (Golden Delicious).

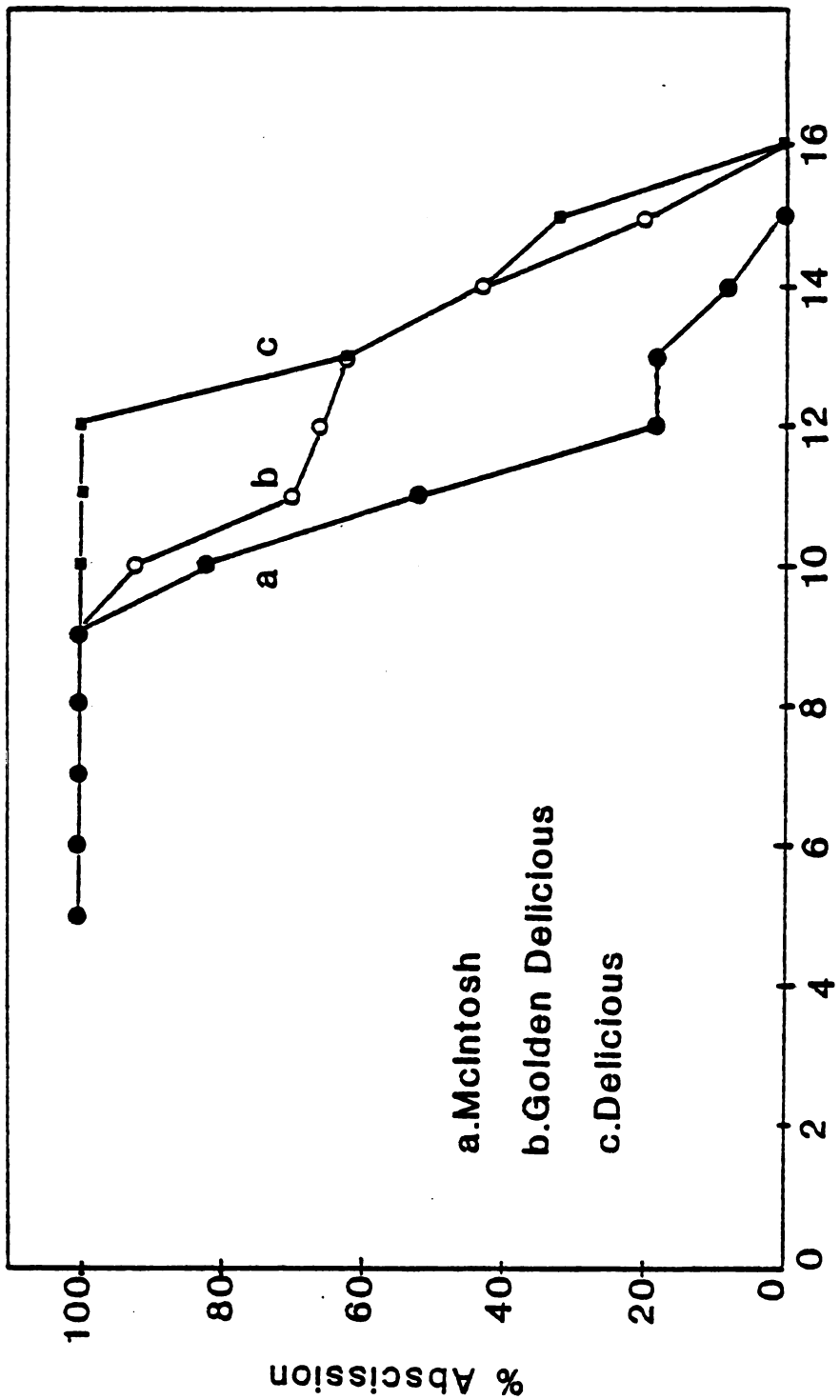
% Abscission
100
80
60
40
20
0
0
2
4
6
8
10
12
14
16
Fruit diameter (mm)
a
b
c
a.McIntosh
b.Golden Delicious
c.Delicious

Figure 1

Figure 2. Relationship between diameter and weight of 'McIntosh' fruits in 1980 and 1981.

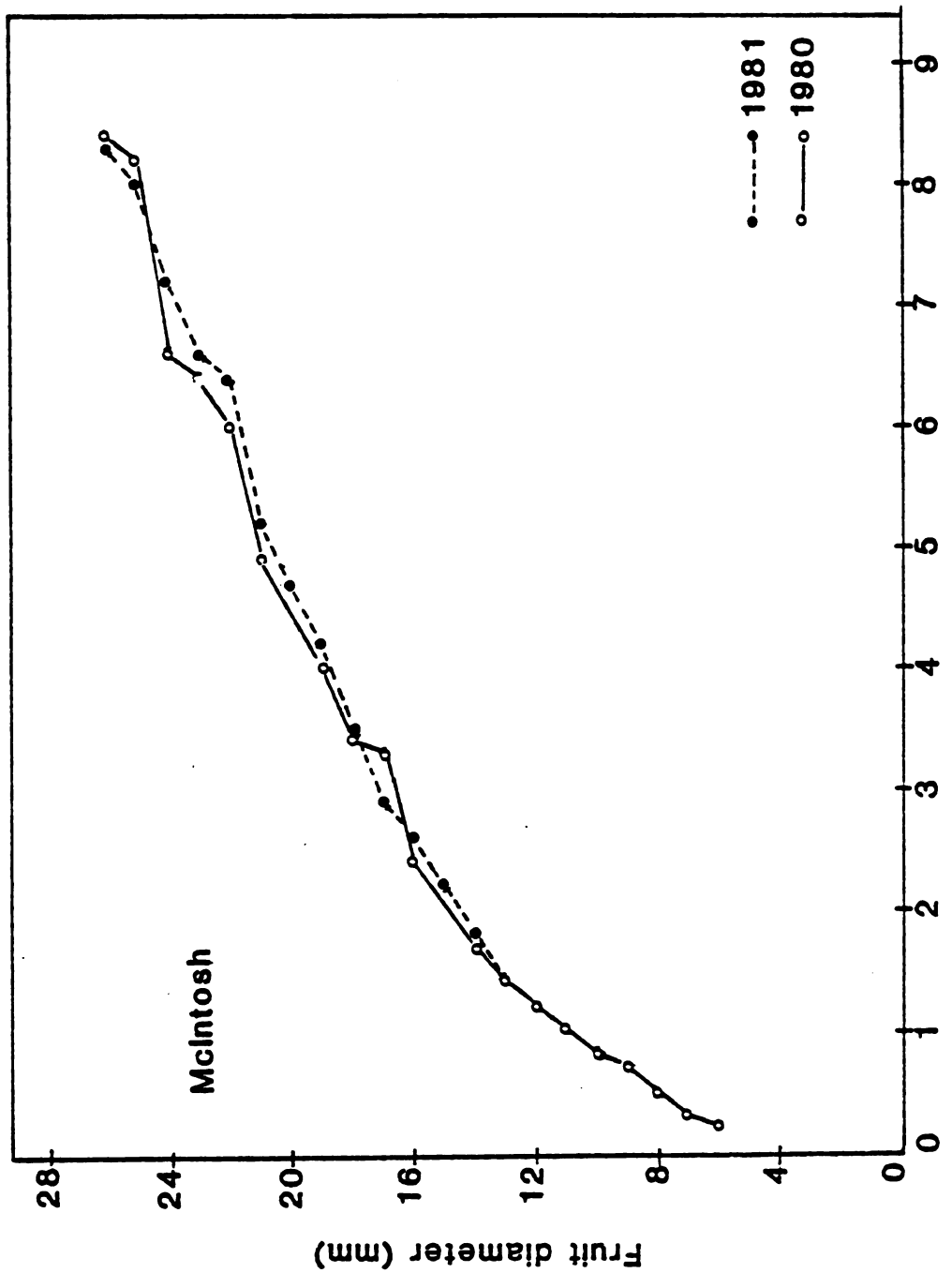
Fruit diameter (mm)
28
24
20
16
12
8
4
0
0
1
2
3
4
5
6
7
8
9
Fruit weight (g)
McIntosh
1981
1980

Figure 2

Table 7. Average fruit weight, diameter, abscission potential and ethylene production of untreated control apple fruits prior to and during "June" drop, 1981.

Sampling Date	Mean Weight (g)	Mean Diameter[z] (mm)	Abscission[y] Potential (%)	C_2H_4 (nℓ/g/hr)
McIntosh			Small fruits	
5/29	1.0	11.0	24	1.22
5/31	0.9	10.5	68	3.03
6/3	1.9	14.8	45	0.73
6/6	2.7	16.4	62	0.84
6/9	4.8	21	6	0.24
			Large fruits	
5/29	1.9	14.8	0	1.21
5/31	1.6	13.6	25	1.03
6/3	2.3	15.8	28	0.69
6/6	3.9	19.0	15	0.39
6/9	7.0	24.2	0	0.13
Red Prince Delicious			Small fruits	
5/31	0.8	9.0	56	0.91
6/2	1.1	10.8	43	2.02
6/5	2.0	13.8	32	1.54
6/8	3.1	16.4	6	1.00
6/11	4.3	18.6	0	0.51
			Large fruits	
5/31	1.4	10.8	4	1.43
6/2	1.7	13.0	18	1.17
6/5	3.2	16.2	0	0.86
6/8	4.6	19.0	0	0.30
6/11	6.3	21.4	0	0.20

[z]Estimated from mean weight using data in Figure 2.

[y]Estimated from mean diameter using data in Figure 3.

Figure 3. Relationship between fruit diameter at various sampling times and fruit abscission as of June 12 (McIntosh) or 14 (Delicious) 1981.

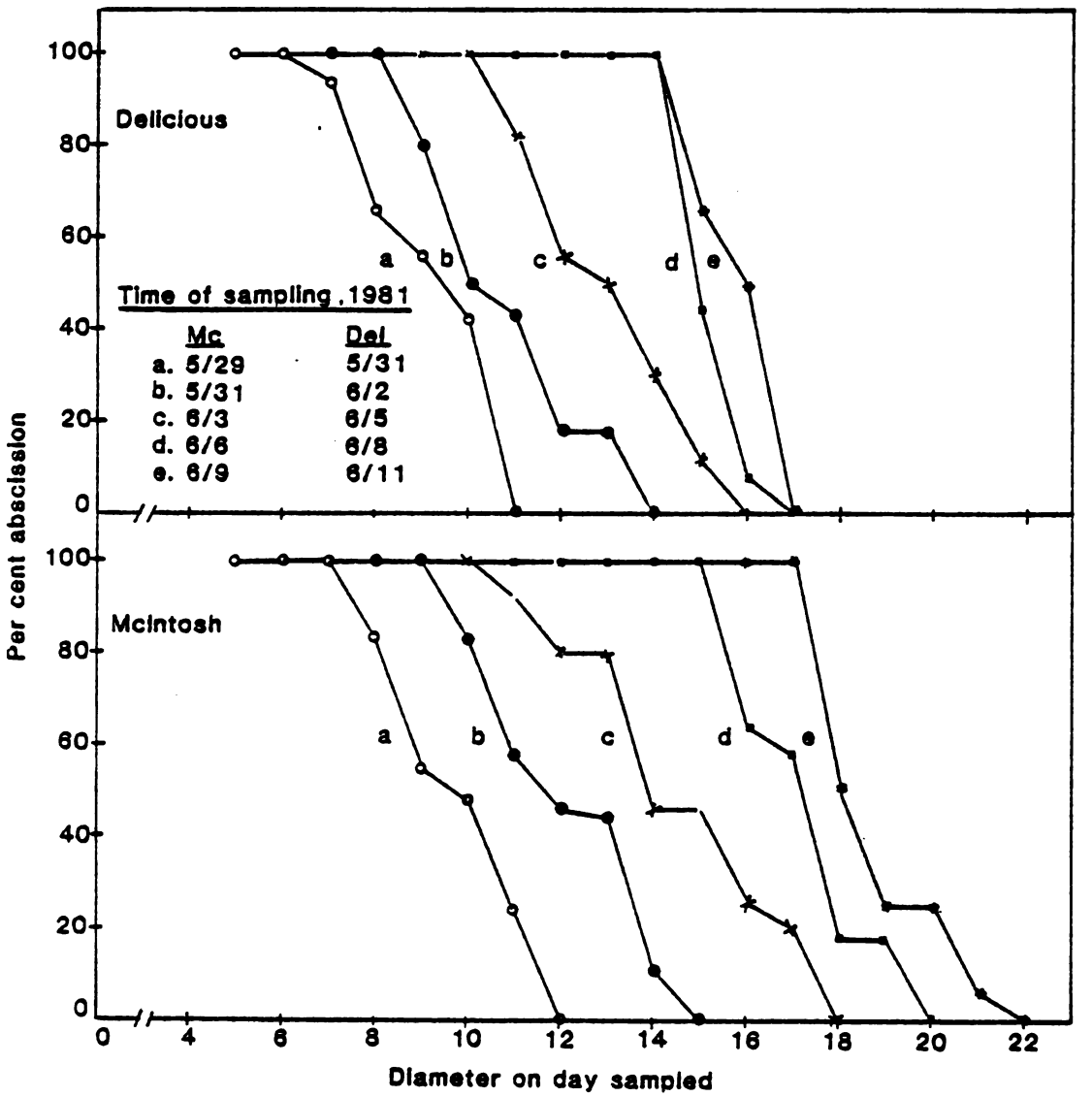
Delicious
McIntosh
Per cent abscission
Diameter on day sampled
Time of sampling, 1981
Mc
Del
a. 5/29
5/31
b. 5/31
6/2
c. 6/3
6/5
d. 6/6
6/8
e. 6/9
6/11
a
b
c
d
e
0
20
40
60
80
100
0
4
6
8
10
12
14
16
18
20
22

Figure 3

Figure 4. Ethylene production by large vs small 'McIntosh' (A + B) and 'Red Prince Delicious' (C + D) apple fruits as a function of day of sampling (A + C) or fruit weight (B + D). Day 0 was May 27 ('McIntosh') or 30 ('Delicious'), 1981.

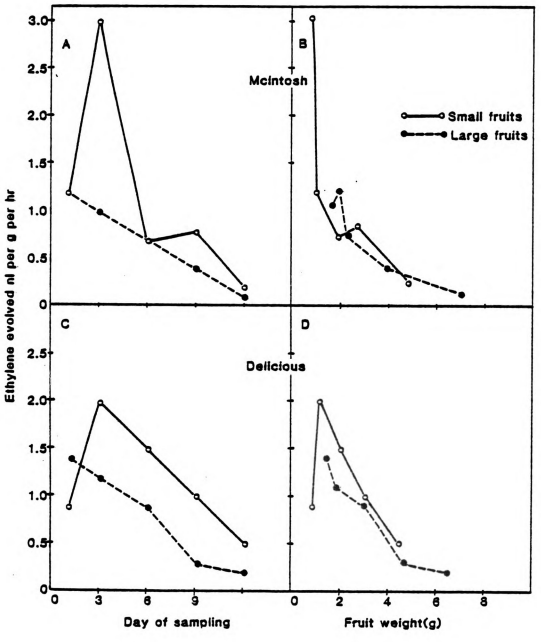
A
B
Mcintosh
Small fruits
Large fruits
C
D
Delicious
Ethylene evolved nl per g per hr
Day of sampling
Fruit weight(g)
3.0
2.5
2.0
1.5
1.0
0.5
0
3
6
9
2
4
8

Figure 4

the other hand, the rate of ethylene evolution declined as fruit size increased; therefore differences in size, per se, could be responsible for differences in ethylene evolution. When the data were replotted as ethylene evolution vs. fruit diameter (Figure 4B and D), the curves for large and small fruits were nearly coincident, suggesting that differences in rates of ethylene production are indeed due to differences in size rather than abscission potential.

Discussion

Williams (1980) suggested that the "June" drop can be reduced or eliminated by inhibiting endogenous ethylene formation; applying AVG at 1000 ppm to apple fruitlets two weeks after full bloom completely eliminated this drop. Although AVG at 200 ppm appeared to increase fruit retention in 4 of 5 comparisons in my experiments (Table 8), the increase was significant in only one of the 4. In a first comparison (1980-McIntosh), AVG actually increased drop significantly. In retrospect either higher concentrations of AVG or more replications should have been used. AVG reduced ethylene evolution from treated fruits in 4 of 5 comparisons (Table 8), all differences being non-significant; furthermore, reductions in ethylene evolution were not necessarily associated with increases in fruit retention.

Table 8. Summary of effects[z] of treatments on apple fruit retention and ethylene evolution 1980-81.

Effects on fruit:	Treatment				
	Scoring	AVG (200 ppm)	Ethephon (200 ppm)	AVG+Ethephon (200 ppm each)	STS (100 ppm)
			'McIntosh', 1980		
Retention	-	-*	--*		
Ethylene evolu.	-	-	++*		
			'Red Prince Delicious', 1980		
Retention	+	+*	--		
Ethylene evolu.	o	-	++*		
			'Golden Delicious', 1980		
Retention	o	+	-		
Ethylene evolu.	-	-	++*		
			'McIntosh', 1981		
Retention		+	-	--+	o
Ethylene evolu.		o	++*	++*	+
			'Red Prince Delicious', 1981		
Retention		+	-	-	o
Ethylene evolu.		-	++*	++*	o

*Significantly different from control at 5% level by DMRT.

[z]- = decrease; + = increase; o = no consistent effect.

Ethephon consistently reduced fruit retention, but the effect was significant only in one case (1980-McIntosh) (Table 8). More pronounced differences were expected in view of the effectiveness of ethephon at 200 or 250 ppm in previous studies with apple (Walsh, et al., 1979; Edgerton and Greenhalgh, 1966; Veinbrants, 1979). For example, Walsh, et al. (1979) increased fruit drop in 'Golden Delicious' and 'Northern Spy' by applying 200 ppm two weeks after petal fall. Ethylene evolution from treated tissues was consistently high following application of ethephon in my experiments, thus breakdown of the chemical did not appear to be limiting activity.

The combined effects of AVG and ethephon paralleled those of ethephon alone, although ethylene evolution was consistently reduced by AVG treatment (Tables 6 and 8). AVG actually increased the thinning effect of ethephon in 'McIntosh' in 1981. Williams (1980 and unpublished data) observed that 400 ppm AVG overcame the promotive effects of NAA (10 ppm) on both fruit abscission and ethylene evolution, but did not reduce the effects of a very high concentration (1000 ppm) of ethephon. These data were interpreted to mean that AVG inhibited the thinning effect of NAA by interfering with NAA-stimulated ethylene synthesis, but was unable to prevent ethephon-induced abscission because biosynthesis of ethylene was not involved.

Neither scoring nor spraying with silver thiosulfate had appreciable or consistent effects on either fruit

retention or ethylene evolution. Limbs may have been scored too late; previous workers treated limbs within two weeks of full bloom (Murneek, 1937; Griggs and Schrader, 1941; Batjer, 1962; Dennis and Edgerton, 1965). Greene (1980) treated apple flowers with $AgNO_3$; ethylene production was stimulated slightly and fruit set was unaffected. However, silver thiosulfate reduces both ethylene evolution and petal abscission in geranium (Miranda, 1981).

Both abscission potential and ethylene production were generally higher in small than in large fruits on a given sampling date (Tables 3, 4, 6). However, ethylene production was more closely associated with fruit size, per se, than with abscission potential (Figure 4). Ethylene evolution decreased as fruit weight increased, confirming the observations of Blanpied (1972), who noted that ethylene content of 'Golden Delicious' fruitlets decreased as growth commenced.

Although these data are not conclusive, they do not support the hypothesis that ethylene production is the controlling factor in apple fruitlet abscission during "June" drop. The effect of ethephon is undoubtedly mediated by the ethylene released within the tissues, but ethylene production in untreated fruits remains far below that observed in ethephon-treated ones within 24 hours of treatment.

The effect of competition between large and small

fruits for nutrients may play a more important role in "June" drop than does ethylene. Abscising fruits generally contain more aborted seeds than adhering ones (Heinicke, 1917; Blanpied, 1972). Hormones probably play a major role in this competition. Young fruits are dependent on their seeds as centers of hormone production for attracting nutrients. Large fruits with more developed seeds probably produce more hormone(s) and can therefore attract more metabolites to them than small ones, and the shedding of fruits occurs at a time when the hormone content of the seeds is low (Luckwill, 1948).

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SECTION III

EFFECT OF AMINOETHOXYVINYLGLYCINE ON THE EFFECTIVE POLLINATION PERIOD OF APPLE

Abstract. Aqueous sprays of aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis, were applied at full bloom to flowers on bagged limbs of 'McIntosh' and 'Delicious' apple (Malus domestica Borkh.) to determine its effect on the effective pollination period. AVG-treated and control flowers were hand pollinated at 1 to 3 day intervals beginning at anthesis. AVG at 200 ppm increased both initial and final fruit set in 'Delicious' but not in 'McIntosh'. In both cultivars, fruit set decreased as the time of pollination was delayed, and response of AVG-sprayed flowers paralleled that of control flowers. These results suggest that AVG has little or no effect on the effective pollination period.

The period during which pollination of the flower results in fertilization is termed the effective pollination period (EPP) (Williams 1965a). It is a function of both ovule longevity and the rate of pollen tube growth. Williams (1965b) reported that EPP, which varied with cultivar and season, was the principal factor controlling fruit set. The EPP of various apple cultivars ranged from 2 to 10 days after anthesis (Williams 1965a).

Ovule longevity is an important factor affecting fertilization. Hough (1947) found that in ovules of 'Delicious' the most frequent abnormality was either a

tardy initiation of the megaspore mother cell or slow rate of development of megaspore and embryo sac. Normal embryo sacs broke down soon after the flower opened even though it had been pollinated with compatible pollen. Hartman and Howlett (1954) found that when pollination of 'Delicious' flowers was delayed until 48 hours after anthesis, fertilization, which seldom occurred in less than 72 hours, was greatly reduced. They attributed this largely to early ovule degeneration. Rootstock may have an effect on embryo sac degeneration. Fruit set of 'Richared Delicious' apple flowers pollinated at full bloom and petal fall was greater in trees propagated on seedling than on M9 rootstocks (Marro, 1976).

Temperature during anthesis influences both pollen tube growth and ovule longevity. Lapins and Arndt (1974) considered the optimum temperatures for pollen tube growth in 'Delicious' flowers to be between 7.2 and 12.8°C; pollen grains failed to germinate below 4.4°. However, low temperatures prolong ovule longevity, increasing the chance of fertilization. Stott (1972) found that ovule longevity ranged from 9 to 12 days after pollination in many apple cultivars and 5 to 6 days were required for compatible pollen tubes to reach the embryo-sac at low temperatures (9.4°). However, tubes required twice as long (12 days) to reach the ovule following self-pollination. Because pollen tubes penetrate more slowly following self-pollination than following cross-pollination, cultivars with a

short EPP are less likely to be self-fruitful than those with a long EPP. EPP was only 3 to 4 days for those cultivars with limited ovule longevity (Stott, 1972). Lapins and Arndt (1974) reported that pollen tubes could reach the base of the style in 3 days at 12.8° vs. 5 days at 7.8°.

In strawberry and lowbush blueberry, pollinated flowers produce more ethylene than non-pollinated flowers (Hall and Forsyth, 1967). In orchids pollination enhances ethylene production and flower fading (Burg and Dijkman, 1967). In carnations pollination of intact flowers promotes endogenous ethylene production and accelerates petal wilting within 2-3 days from pollination (Nichols, 1977). The role of ethylene in regulating EPP and ovule longevity has not been investigated. However, inhibitors of ethylene synthesis such as aminoethoxyvinylglycine (AVG) both increase fruit set and inhibit ethylene evolution in apple (Dennis et al., 1978; Greene, 1980; Williams, 1980).

The purpose of this study was to determine the role of AVG on EPP in 'Delicious' and 'McIntosh' apple flowers.

Materials and Methods

Experimental Procedure

Eight uniform branches per tree were selected on three 'Starking Delicious' and three 'McIntosh' apple trees about 40 years old in a commercial orchard at Leslie, MI

in 1981. These branches were enclosed in cheesecloth bags before full bloom (pink stage) to prevent pollination by insects. At full bloom the "king" flower and all frost-damaged flowers were removed and about 100 viable flowers were counted on each branch. Four branches on each tree were sprayed with AVG (200 ppm) at full bloom (May 6 for 'McIntosh'; May 8 for 'Delicious') and four branches were left untreated. The following pollination treatments were randomly assigned to four AVG-treated and four control limbs on each tree, using a randomized block design with trees as blocks: hand pollinated 0, 2, 5 or 6 days (McIntosh) or 0, 3, 4 and 5 days ('Delicious') after AVG application, using pollen previously collected from 'Empire' apple flowers. All limbs remained bagged, except at the time of pollination, until 10 days after each treatment. The flowers were counted at the time of pollination and initial and final set were recorded. Ten fruits were harvested at maturity from each treated and non-treated limb and the length, diameter and seed number were determined for each fruit.

Results

In 'McIntosh', both initial and final set declined as pollination was delayed (Table 1; Figure 1), the effect becoming significant after 5 (initial) or 6 days (final

Table 1. Effect of AVG on effective pollination period and fruit characteristics at harvest of 'McIntosh', Leslie, MI 1981. Flowers on bagged limbs treated with AVG (200 ppm) at full bloom (May 6).

AVG (ppm)	Time of hand pollination (day after full bloom)				
	0	2	5	6	Mean
			Initial set[z] (%), 5/27		
0	71	62	40	23	49 1[y]
200	78	78	44	28	57 1
Mean	75 a[y]	70 a	42 b	26 b	
			Final Set[z] (%), 6/16		
0	35	20	17	9	20 1
200	21	33	22	15	23 1
Mean	28 a	27 a	19 ab	12 a	
			Seeds per fruit, 9/14		
0	4.7	5.2	4.1	4.0	4.5 1
200	3.9	4.7	3.8	3.6	4.0 1
Mean	4.3 a	5.0 a	3.9 a	3.8 a	
			Fruit weight (g), 9/14		
0	126.3	116.0	098.0	101.7	110.5 1
200	90.3	95.7	98.7	86.3	92.6 m
Mean	108.3 a	105.8 a	98.3 a	94.0 a	
			L/D ratio, 9/14		
0	.80	.78	.79	.78	.79 1
200	.80	.82	.81	.80	.81 m
Mean	.80 a	.80 a	.80 a	.79 a	

[z]Fruits per 100 flowers.

[y]Mean separation within rows, observations, and sets by DMRT, 5% level.

Figure 1. Effect of AVG on effective pollination period (E.P.P.) of 'McIntosh' and 'Starking Delicious' apple 1981. AVG (200 ppm) applied May 6 ('McIntosh') or 8 ('Starking Delicious') to bagged limbs. Flowers hand-pollinated with 'Empire' pollen at indicated times. Broken lines indicate initial set of AVG-treated (a) and control (b) flowers, solid lines final set of AVG-treated (c) and control (d) flowers.

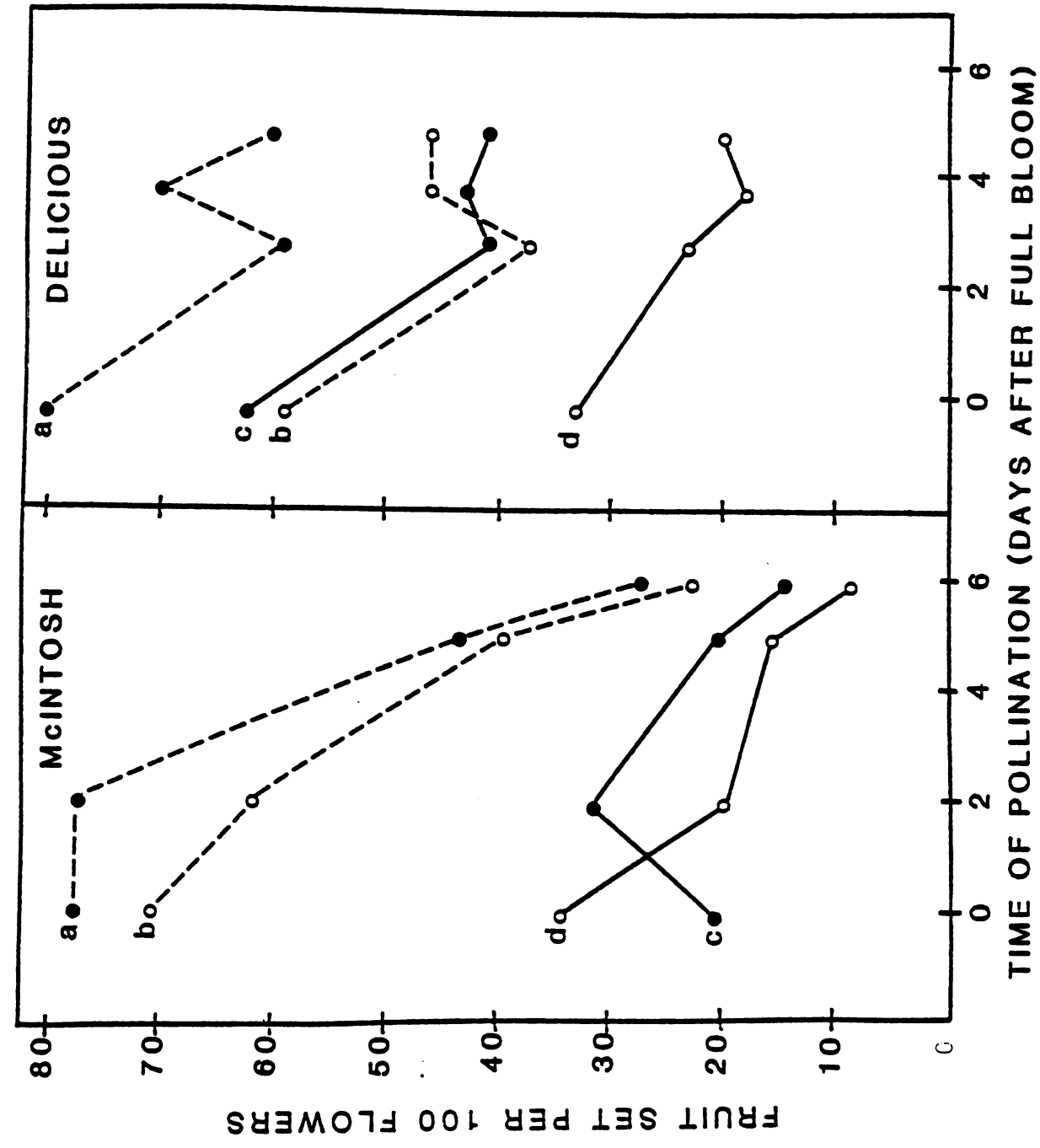
DELICIOUS
McINTOSH
a
b
c
d
FRUIT SET PER 100 FLOWERS
80
70
60
50
40
30
20
10
0
2
4
6
TIME OF POLLINATION (DAYS AFTER FULL BLOOM)

Figure 1

set). AVG did not increase set significantly in 'McIntosh' regardless of time of pollination, but did reduce fruit size and increase L/D ratio.

In 'Delicious' although fruit set was highest when flowers were pollinated at full bloom, time of pollination did not significantly affect either initial or final set (Table 2, Figure 1). However, AVG increased both initial and final set significantly. Fruits from AVG-treated flowers were smaller than control fruits except those from flowers pollinated 6 days after full bloom, but the effect was not significant at 5%. Neither seed number per fruit nor L/D ratio was altered by AVG.

Interaction between AVG treatment and time of pollination was not significant in either cultivar. If AVG increases ovule longevity, it should prolong the period during which pollination is effective, resulting in a greater response relative to the control as pollination is delayed. Because fruit set of control flowers declined with time, the basis of comparison for the effect of AVG also declined. To determine if relative response to AVG increased as pollination was delayed, response was plotted as per cent of the control (no AVG) as a function of time of pollination. The results (Figure 2) again indicate no consistent change in response to AVG with time.

Table 2. Effect of AVG on effective pollination period and fruit characteristics at harvest of 'Starking Delicious', Leslie, MI 1981. Flowers on bagged limbs treated with AVG (200 ppm) at full bloom (May 8).

AVG (ppm)	Time of hand pollination (days after full bloom)				
	0	2	5	6	Mean
			Initial set[z] (%), 5/30		
0	59	37	46	46	47 1[y]
200	80	59	70	60	67 m
Mean	69 a[y]	48 a	58 a	53 a	
			Final set[z] (%), 6/16		
0	33	23	18	20	23 1
200	62	41	43	41	47 m
Mean	48 a	32 a	31 a	30 a	
			Seeds per fruit, 10/2		
0	5.1	6.3	5.7	6.0	5.8 1
200	5.3	4.9	5.8	5.7	5.4 1
Mean	5.2 a	5.6 a	5.7 a	5.9 a	
			Fruit weight (g), 10/2		
0	115.7	116.3	120.0	107.0	114.8 1
200	103.7	98.7	103.3	115.0	105.2 1
Mean	109.7 a	107.5 a	111.7 a	110.0 a	
			L/D ratio, 10/2		
0	.99	.99	.96	.99	.98 1
200	.99	.99	.97	.97	.98 1
Mean	.99 a	.99 a	.96 a	.98 a	

[z]Fruits per 100 flowers.

[y]Mean separation within rows, observations, and sets by DMRT, 5% level.

Figure 2. Fruit set in response to AVG expressed as percent of the control as a function of time of pollination.

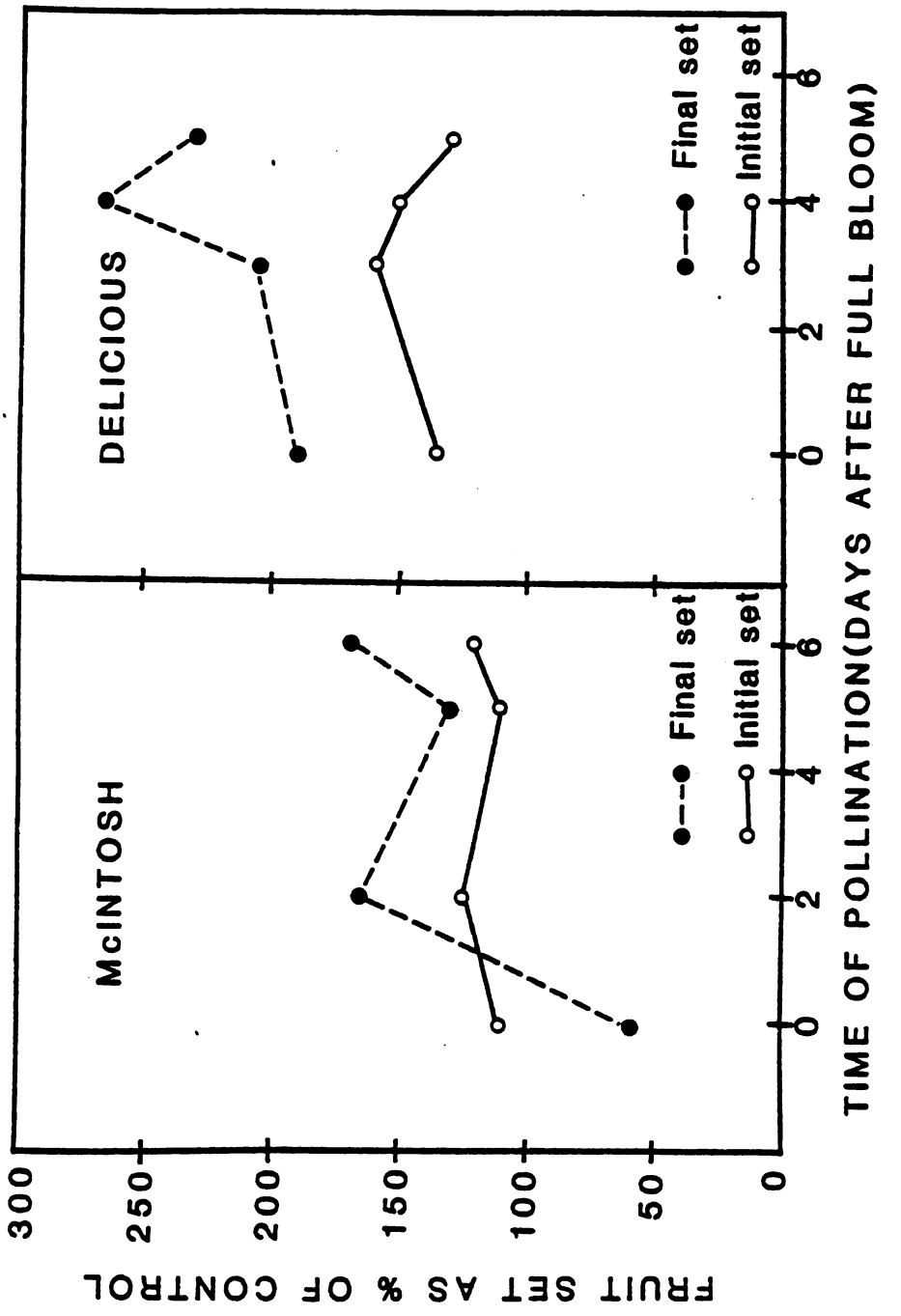
FRUIT SET AS % OF CONTROL
300
250
200
150
100
50
0
McINTOSH
DELICIOUS
Final set
Initial set
0
2
4
6
TIME OF POLLINATION(DAYS AFTER FULL BLOOM)

Figure 2

Discussion

If AVG increased set by prolonging ovule longevity, a significant interaction should be observed between AVG treatment and time of pollination; specifically, the decline in set should be more rapid in untreated than in treated flowers.

The results of this experiment varied with cultivar. In 'McIntosh', although final set was higher in AVG-treated flowers in 3 of the 4 comparisons (times of pollination), its effects were statistically non-significant overall. The effect, if indeed real, actually declined with time of pollination. Although the effect of AVG was significant in 'Delicious', the magnitude of the response did not change with time of pollination (Figure 1). Thus the data do not support the hypothesis that AVG prolongs the EPP.

Two results are surprising in view of previous reports. First, 20% of the 'Delicious' flowers were still capable of setting fruit when pollinated 5 days after full bloom, yet Hartman and Howlett (1954) reported drastic reductions in set when pollination was delayed only 48 hours. In 'Delicious' low temperatures (7.8, 3.9, 2.8, 8.3°C) during time of pollination might have prolonged ovule longevity, especially in those flowers pollinated 3 and 4 days after full bloom. Considering the high response of 'Delicious' flowers to AVG the experiment might have been prolonged

for several more days. Secondly, percent set in control 'McIntosh' flowers was no better than in 'Delicious', despite previous reports (e.g., Dennis, 1979) of poorer set in the latter. A freeze prior to bloom killed considerably more 'McIntosh' than 'Delicious' flowers; if sub-lethal injury paralleled lethal injury, the viability of the surviving flowers may have been lower in 'McIntosh' than in 'Delicious'.

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SECTION IV

THE EFFECT OF SUPPLEMENTARY HAND POLLINATION ON FRUIT SET AND POLLEN TUBE GROWTH IN APPLE

Abstract. Hand-pollination of open-pollinated flowers of 'Delicious' and 'McIntosh' apple (Malus domestica Borkh.) with 'Empire' pollen at full bloom increased initial and final fruit set in 'Delicious' but not in 'McIntosh'. Bagged limbs set only 0.4 to 1 fruit per 100 flowers. Staining with aniline blue made pollen tubes visible in the entire length of 'McIntosh' styles, but none were observed at the base of 'Delicious' styles. Pollen tubes in open- and open- plus hand-pollinated flowers reached the base of 'McIntosh' styles within 4 to 6 days, but almost none reached the base in self-pollinated (bagged) flowers, and most were swollen and terminated in callose plugs. These results are discussed in relation to the role of "basal gaps" between the stamens in limiting fruit set of 'Delicious'.

The beneficial effect of cross-pollination on fruit set of some fruits was recognized as early as 1824 (Swayne, 1824). Most of the apple cultivars in the eastern United States are self-incompatible; a biochemical antagonism prevents pollen grains from germinating on, or growing into, the stigmas of the same variety. Some cultivars such as 'Golden Delicious', 'Rome Beauty' and 'York Imperial" are self-fruitful, but crop more consistently with cross-pollination (Way 1978).

'Delicious' is totally self-unfruitful (Howlett, 1928; Overholser and Overly 1931; Roberts, 1945) and cross-pollination is essential for consistent heavy production. Howlett (1929) found that limited fruit set in 'Delicious' was due in large part to inadequate pollination.

Flower structure was recognized as a limiting factor in 'Delicious' pollination as early as 1945. Roberts (1945) reported that the structure of 'Delicious' blossoms permits honey bees to remove nectar without transferring pollen to the stigma; only about 20 percent of the bees visiting the flowers crawled over the stigmata. Robinson (1979) reported similar "sideworking" of honey bees on 'Delicious' blossoms as a result of "basal gaps" or spaces between the stamens. The maximum width of the tongue (glossa) of a honey bee is about 180 µm. Basal gaps greater than 180 µm were found to be much more abundant in 'Delicious' sports than in 11 other cultivars (Robinson, 1979). Robinson concluded that the behavior of honey bees on apple blossoms is determined by the presence or absence of these basal gaps, which reduce the rate of cross-pollination.

Supplementary pollination is a potential method for enhancing fruit set, but the cost would probably be prohibitive. Williams (1970) compared the effects of supplementary hand pollination on fruit set of 'Cox's Orange Pippin' apple in England. The average number of fruits

per 100 flower clusters for 21 'Cox' orchards was 33.1 for those receiving supplementary pollination (one flower hand pollinated per 4 clusters) vs. 25.6 for controls with natural pollination only. Supplementary pollination increased yield by an average of 29%. Increased fruit set may have been the result of a higher number of pollen grains per stigma as well as more cross-pollinated flowers. Theoretically only a few pollen grains per flower are required for fertilization; however, Forshey (1978) suggested that 'Delicious' flowers must be saturated with pollen because a relatively low percentage of pollen tubes actually reach the embryo sac. Lapins and Arndt (1974) reported that the presence of fewer than about 50 pollen grains on the stigma usually resulted in poor germination of pollen, slow growth of pollen tubes, and poor set of fruit. However, they did not present supporting data.

Another factor which may affect pollen tube growth is double pollination. Visser and Verhaegh (1980) pollinated 'Golden Delicious' flowers twice within one or two days. By using scab-resistant pollen parents and recording the proportion of seeds which produced scab resistant seedlings, they demonstrated that an average of 37% of the seeds originated from the first and 63% from the second pollination. They proposed that pollen tubes grew more rapidly in styles which had been previously penetrated by pollen tubes, and were therefore more effective in fertilization.

The purposesof this study were (a) to evaluate the importance of basal gaps in 'Delicious' flowers by comparing the effects of supplementary hand pollination on fruit set in 'Delicious' vs. 'McIntosh' (which lacks such gaps), and (b) to compare the rates of pollen tube growth in the styles of these two cultivars.

Materials and Methods

Three uniform branches were selected on each of 3 'Starking Delicious' and 3 'McIntosh' apple trees approximately 40 years old in a commercial orchard at Leslie, MI. One limb on each tree was enclosed in a cheesecloth bag prior to flower opening to exclude insects. At full bloom all "king" (terminal) and frost-injured flowers were removed from each branch, and the remaining lateral flowers were counted. The following treatments were applied, using a randomized block design with trees as blocks: bagged to prevent pollination by insects; open-pollinated; and open-pollinated plus hand-pollinated. All flowers in the last treatment were hand-pollinated at full bloom using pollen collected 48 hours previously from 'Empire' apple flowers. The terminal 75 to 100 flowers on the branch were used to record fruit set and 30 to 50 flowers were collected from each branch 1, 2, 3, and 4 days after full bloom. The flowers were fixed within half

an hour of collection in formalin: acetic acid: 80% ethanol (FAA) (1:8:1 by volume) (Johansen, 1940), for subsequent evaluation of pollen tube growth. The styles were subsequently rinsed with tap water, placed in an aqueous solution of 3N NaOH overnight to clear and soften the tissue, rinsed in tap water for one hour to remove the sodium hydroxide, then held for 18 to 24 hr in a solution of 0.1% aniline dissolved in 0.1 N K_3PO_4 (1 gm aniline + 7.072 gm K_3PO_4 per ℓ) at room temperature. The styles were placed on a slide in a few drops of glycerine, covered with a cover slip and squashed. The prepared slides were viewed under a Nikon-AFM photomicroscope with epi fluorescence. Ektachrome 200 film was used to record pollen tube penetration into the style.

Results

Effect of supplementary pollination on fruit set. Bagged flowers set very few fruits (Table 1). Supplemental hand pollination approximately tripled initial set and doubled final set in comparison with open-pollination in 'Delicious', but had no significant effect in 'McIntosh' (Table 1). The 'June' drop was considerably heavier in 'McIntosh' than in 'Delicious' despite similar fruit loads on hand-pollinated limbs.

Table 1. Effect of supplemental hand pollination on fruit set of apple at Leslie, MI 1981.

Treatment[z]	No. of flowers	Fruits per 100 flowers: Initial		Fruits per 100 flowers: Final	
		'McIntosh'			
Bagged	58	3	b[y]	1	b
Open-pollinated	81	60	a	20	a
Open + hand pollinated[x]	88	65	a	21	a
		'Starking Delicious'			
Bagged	109	1	c	0.4	c
Open pollinated	136	24	b	17	b
Open + hand pollinated	106	68	a	41	a

[z]One limb on each of 3 trees per treatment.

[y]Mean separation within columns and cultivars by DMRT, 5% level.

[x]Hand pollination with 'Empire pollen on May 6 (McIntosh) or May 8 (Delicious).

Germaination of pollen and growth of pollen tubes in the style. Pollen grains and pollen tubes fluoresced a brilliant yellow under ultraviolet light following staining with aniline (Figures 1 and 2). However, a marked difference between cultivars was evident in the staining of tubes in the basal half of the style. In 'Delicious' no pollen tubes were observed in the base of any styles (Figure 2), even 5 days after full bloom, despite the fact that fruit set was normal to heavy (Table 1, Figure 2).

In open-pollinated and open- plus hand-pollinated 'McIntosh' flowers many pollen tubes reached the base of the style within 4 to 6 days of full bloom (Table 2 and Figure 1). Pollen tube growth did not appear to differ in styles of open- vs. open-plus hand-pollinated flowers. Few pollen tubes were evident in the styles of bagged flowers in either cultivar and the few tubes present had highly callosed terminal plugs (Figures 1 and 2). No pollen tubes reached to the base of the style within 6 days after full bloom.

Discussion

If basal gaps limit set in 'Delicious', set of open-pollinated flowers should be lower and hand-pollination should have a greater effect in this cultivar than in

Figure 1. Appearance of pollen tubes in 'McIntosh' apple styles under ultraviolet light after staining with 0.1% aniline blue in 0.1 N K_3PO_4. a and b self-pollinated; c and d open-pollinated; e and f open and hand pollinated. Flowers collected 2 (A,C,E) or 6 (B,D,F) days after hand pollinating at full bloom. Abrupt termination of fluorescence in (D) indicates point at which style was severed.

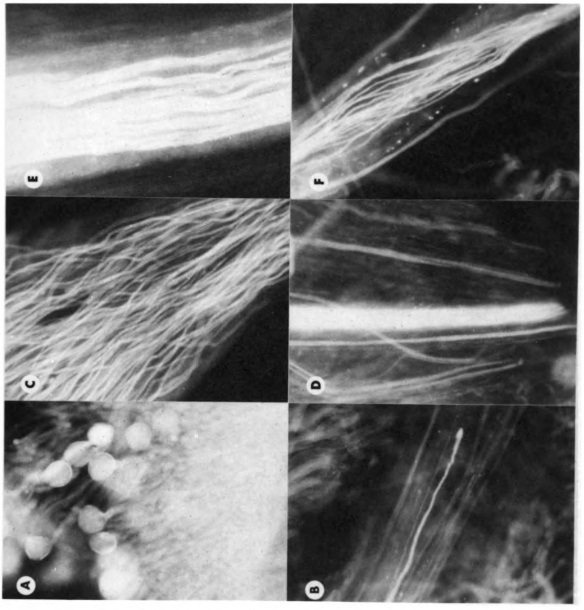
A
B
C
D
E
F

Figure 2. Appearance of pollen tubes in 'Starking Delicious' apple under ultraviolet light after staining with 0.1% aniline in 0.1 N K_3PO_4. a and b self-pollinated; c and d open pollinated; e and f open- plus hand-pollinated. Flowers collected 3 (A,B,C) or 6 (B,D,F) days after hand-pollinating at full bloom.

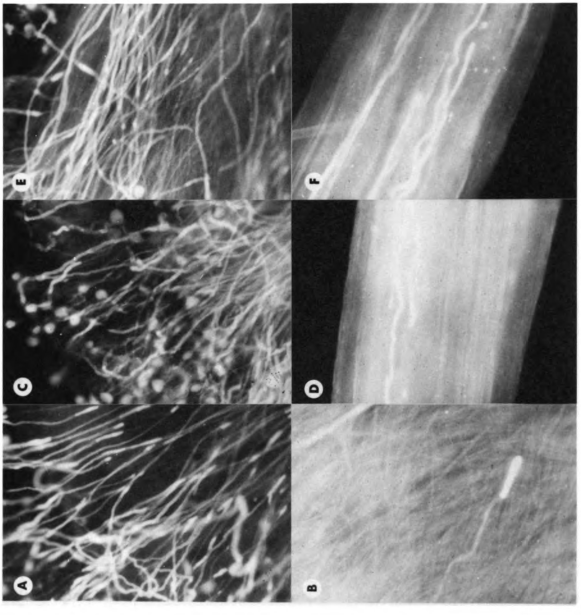
A
B
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Table 2. Effects of self- (S), open- (O), and open-plus hand- (O+H) pollination on pollen germination and tube growth in apple flowers, 1981, as determined by staining with aniline.

Treatment	Days after Full Bloom	% of Flowers[y] in Which: Pollen had Germinated	Pollen tubes had reached indicated % of style length			
			25	50	75	100
		'McIntosh'				
S[x]	2	40				
O		91	81	33	12	2
O+H[z]		73	53	33	13	4
S[x]	5	86	86	86	86	-
O		85	85	85	85	70
O+H[z]		100	100	100	100	91
S[x]	6	92	92	92	92	4
O		87	87	87	87	87
O+H		89	89	89	89	89
		'Delicious'				
S[x]	3	36	18	6	0	0
O		50	37	6	00	0
O+H[z]		88	76	36	0	0
S[x]	4	67	17	4	0	0
O		90	90	61	0	0
O+H[z]		100	100	36	0	0
S[x]	6	68	68	0	0	0
O		100	100	9	0	0
O+H[z]		96	96	25	0	0

[z]Hand-pollination with 'Empire' pollen at full bloom on May 6 ('McIntosh') or 8 ('Delicious').

[x]Limbs bagged prior to flower opening.

[y]Approximately 30 to 50 flowers per observation.

'McIntosh', which has fewer such gaps. Data for initial set (Table 1) support this hypothesis, for open-pollinated 'Delicious' flowers set only one-third as many fruits as 'McIntosh' flowers, and hand-pollination had a dramatic effect in 'Delicious' but no effect in 'McIntosh'. Data for final set paralleled that for initial set, except that the heavy 'June' drop in 'McIntosh' caused final fruit set on open-pollinated branches to be no greater than in 'Delicious'. The results therefore are inconclusive.

Comparison of pollen tube growth in self- vs open-pollinated flowers supports previous observations (Stott, 1972) on the growth of incompatible and compatible pollen tubes in apple. Swollen and highly callosed terminal plugs, together with stoppage of growth in the upper portion of the style, indicated self-incompatibility in bagged flowers. In contrast, pollen tubes in open-pollinated styles had no terminal plugs, grew rapidly, and reached the base of the style in 'McIntosh' flowers within 4 to 6 days (Figure 1). The failure to observe pollen tubes in the base of 'Delicious' styles following open-pollination is difficult to explain in view of the fact that fruit set occurred. Apparently chemical components in the stylar tissue or physical obstructions to penetration of the dye prevented reaction with the callose of the pollen tube.

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SUMMARY AND CONCLUSIONS

To test the hypothesis that endogenous ethylene inhibits fruit set in apple, aminoethoxyvinylglycine (AVG), an inhibitor of ethylene synthesis and (2-chlorethyl) phosphonic acid (ethephon), an ethylene-generating compound, were applied to branch units of 'McIntosh', 'Red Prince Delicious' and 'Golden Delicious' apple trees at full bloom in 1980 and 1981. When applied directly to the flower clusters at full bloom, AVG at 200 ppm significantly increased both initial and final fruit set in all three cultivars in 1980 and initial fruit set in 'Delicious' and 'Golden Delicious' in 1981. The effects of 100 ppm were generally non-significant. AVG at 200 ppm significantly reduced fruit weight in 'McIntosh' and 'Delicious' in both years but had no effect on seed number and fruit retention. AVG at both concentrations reduced ethylene evolution from flowers excised 1 to 10 days after treatment, but the effects were not statistically significant at the 5% level. Ethephon (40 to 100 ppm) had no significant effect on fruit set, yet significantly increased ethylene production. 'Delicious' flowers consistently responded less to ethephon than did 'McIntosh' and 'Golden Delicious' flowers. The pH of 'Delicious' flowers may be lower, resulting in less breakdown of ethephon in the tissues. AVG had little effect on ethylene synthesis but markedly increased fruit set,

while ethephon increased ethylene evolution but did not affect fruit set. Therefore the effect of AVG on fruit set appears to be independent of its ability to inhibit ethylene synthesis. In order to better understand the relationship between fruit set and ethylene evolution, a wider range of concentrations of AVG and ethephon should be applied using more replicates to reduce variability.

To determine the effect of AVG on the effective pollination period aqueous sprays of AVG were applied at full bloom to flowers on bagged limbs of 'McIntosh' and 'Delicious' apple trees. AVG-treated and control flowers were hand-pollinated with 'Empire' pollen at 1 to 3 day intervals beginning at anthesis. AVG (200 ppm) increased fruit set in 'Delicious' but not in 'McIntosh'. Fruit set decreased as the time of pollination was delayed, and the response of AVG-treated flowers paralleled that of control flowers. These results suggested that AVG has little or no influence on the effective pollination period. However the experiment should be repeated, extending the time of pollination up to 10 days after anthesis.

To test the hypothesis that "basal gaps" between the stamens of 'Delicious' flowers limit fruit set by permitting bees to obtain nectar without transferring pollen to the stigma, supplemental hand pollination was used on open-pollinated flowers of 'McIntosh' and 'Delicious' at full bloom. Hand pollination increases fruit set in 'Delicious'

but not in 'McIntosh', supporting the hypothesis. However, final set of open-pollinated flowers was no greater in 'McIntosh' than in 'Delicious' staining with aniline blue made pollen tubes visible in the entire length of 'McIntosh' style, but only in the upper half of 'Delicious' styles. Many pollen tubes in open- and open- plus hand-pollinated flowers reached the base of 'McIntosh' styles within 4 to 6 days but none were observed at the base of 'Delicious' styles.

Application of AVG (200 ppm) 18 to 21 days after full bloom had no significant effect on ethylene evolution from fruitlets. Although AVG significantly increased fruit drop in 'McIntosh' and reduced it in 'Delicious' in 1980, it had no significant effects in 1981. Neither silver thiosulfate (100 ppm) nor scoring had consistent effects on either set or ethylene evolution.

Ethephon at 200 ppm significantly increased ethylene evolution and reduced fruit retention in all three cultivars but 100 ppm was effective only in 'McIntosh' and 'Golden Delicious'. Small fruits had a higher abscission potential and generally produced more ethylene than large fruits. The rate of ethylene production of non-treated fruits generally declined with both date of sampling and fruit weight. The results of this study suggested that differences in the rate of ethylene evolution were due to differences in size rather than to differences in abscission

potential. Therefore ethylene is probably not the primary factor responsible for "June" drop. The auxin content of immature seed, flesh, and pedicel tissue may be better correlated with fruit drop than is ethylene production.

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