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THE RELATIONSHIP BETWEEN FRUIT SET OF APPLE AND CARBOHYDRATE CONTENT OF BARK AND FLOWER CLUSTER BASE TISSUES

By

Darcy Camelatto

A DISSERTATION

Submitted to Michigan State University in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

Department of Horticulture

ABSTRACT

THE RELATIONSHIP BETWEEN FRUIT SET OF APPLE AND CARBOHYDRATE CONTENT OF BARK AND FLOWER CLUSTER BASE TISSUES

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Apple tissues were analyzed to determine the relationships between carbohydrate content and fruit setting ability. Shading was employed to reduce carbohydrate content and scoring or girdling to increase it. Additional comparisons were made of a) strains of 'Delicious' apple that differ in fruit setting ability, b) trees on rootstocks that affect fruit set, and c) Starkrimson 'Delicious' trees in commercial orchards with varying cropping potential.

Bark discs were removed from 1-year-old wood at bloom and at intervals thereafter, and flower cluster bases were collected at bloom. All tissues were oven-dried and extracted with 80% ethanol. Gas chromatography was used to quantify free sugars and sugar alcohols. Residual starch was enzymatically hydrolyzed and glucose in the hydrolysate determined spectrophotometrically.

Shading [30% (= 70% full sun)] was ineffective in reducing levels of carbohydrates or fruit set of Redchief 'Delicious' whether applied in spring or fall. Although 60% shade reduced both initial and final set, carbohydrate content was not reduced significantly until 15 days after bloom. Scoring of the trunk at full bloom had no significant effect. In a second experiment with 'Empire' and 'MacSpur' trees, 60 and 85% shade reduced set, but carbohydrate content was not reduced until 25 days after bloom. Girdling of the trunk reduced set without affecting carbohydrate content appreciably at the time of "June" drop.

'Imperial Red Delicious' trees on MAC 9 (dwarfing) rootstocks set a larger percentage of their flowers than did trees on MAC 11 or MAC 24 (both semi-vigorous). However, effects of rootstock on carbohydrate content were inconsistent. 'Empire' trees on M.111 rootstocks were also compared with similar trees with M.8 and M.9 (both dwarfing) interstems. Although both interstems increased set, only M.9 increased carbohydrate content.

Comparison of several strains of 'Delicious' that differ in productivity indicated that carbohydrate content was often higher in poorly setting strains. Analysis of data for 4 commercial orchards indicated positive correlations between fruit set and carbohydrate content of cluster bases, but not of bark tissue.

In summary, although content of carbohydrates, especially sorbitol and sucrose, was sometimes positively correlated with fruit set, many exceptions were found. Thus carbohydrate content alone is not a reliable indicator of fruit setting potential. To my loving wife

Neli

and children

Patricia, Tiago, and Patrick

To my mother Dusolina and to the memory of my father Eugenio

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INTRODUCTION

The setting of fruits is essential for commercial success in tree fruit production. Once the fruits have set, other treatments can be applied to improve fruit size and quality and thereby maximize profits.

Several factors are involved in fruit set of temperate fruit trees. Climatic conditions can interfere with crosspollination, frost can injure flower parts, and solar radiation, nutrition and other cultural practices (pruning, training, growth regulators, pest control, etc.) can affect fruit set.

Considerable evidence exists in the literature that carbohydrates are important in the setting of apple fruits. Relatively high temperatures during late winter and early spring can reduce fruit set of apple. Such temperatures may reduce carbohydrate availability to flowers and growing fruitlets, since high temperatures increase respiration and therefore more carbohydrate reserves are consumed.

Post-bloom application of shade, as well as treatment with photosynthetic inhibitors, can cause abscission of fruitlets which have reduced content of carbohydrates. On the other hand, post bloom injection of sorbitol increases fruit set and can overcome the deleterious effects of shade.

Other factors that affect fruit set include rootstock, interstem, strain, girdling and scoring. These could also influence carbohydrate content.

My purpose was to establish whether the effects of several treatments/cultural practices that affect fruit set could be explained by their effects upon carbohydrate content of either cluster bases or bark tissues. Shading was applied to apple trees to reduce carbohydrate content, and girdling to increase it. Experiments involving different rootstocks, interstems, and strains of 'Delicious' were also performed, and fruit set was recorded. Fruit set was also recorded in several commercial orchards in Michigan. In all these experiments, cluster bases and bark tissue of oneyear-old branches were analyzed in order to determine the relationship between carbohydrate content and fruit set.

I. LITERATURE REVIEW

A. Fruit Set of Apple

Fruit set may be defined as "the proportion of flowers which give rise to fruits", while "initial set" refers to the initial swelling of the ovary, and "final set" to the production of mature fruits (Dennis, 1984). For my purposes, initial set will be defined as the proportion of flowers forming fruitlets that remain on the tree for at least 20 days after full bloom (DAFB), and final set as the proportion of flowers forming fruits that remain on the tree after "June drop". In apple, two post-bloom periods of fruitlet abscission are usually recognized: "first drop", that occurs in two waves of fruitlet abscission, one immediately after bloom, and a second that occurs at approximately 2 to 3 weeks after bloom, and "June" drop (Childers, 1969; Gourley and Howlett, 1957; Teskey and Shoemaker, 1972). Heinicke (1917) stated that many of the flowers are lost a few days after petal fall, and a large number of partially developed fruits abscise during the next few weeks. A rather conspicuous drop, commonly called "June" drop occurs in June and July when the fruits are from one to three centimeters in diameter. Although fruit size is important, fruit set is often the most important factor controlling productivity in apple. Dennis (1981 b)

considered fruit set to be the major factor limiting yield of 'Delicious' apple.

1. Effects of environmental factors.

Temperature. Temperatures previous to, during and after bloom affect fruit set of apples. Low temperatures can decrease fruit set of pollinated flowers by injuring pistils and/or pollen, and also by decreasing the rate of pollen tube growth (Boyd and Latimer, 1933). Injured flowers can sometimes survive after cold injury, but their setting ability is decreased (Forshey, 1978; Wilson and Williams, 1970). Pollen grains of 'Delicious' apple fail to germinate at temperatures below 4.4C (Lapins and Arndt, 1974). These authors also observed that pollen tubes of that cultivar reached the base of the style in 3 days at a continuous temperature of 12.8C vs. 5 days at 7.2C.

All apple cultivars are self-incompatible to some degree (Janick and Moore, 1975). Therefore, interplanting of trees of different cultivars that produce intercompatible pollen is a general rule in apple orchards. Since wind pollination is not effective in apple, cross-pollination is dependent upon insects (Robinson, 1980). Among insects, honey bees are the main pollinators in apple orchards (Hoffman 1966; Wilson and Williams, 1970). Therefore, cross-pollination in apple depends upon bee activity, which can be affected by temperature. Bee activity during apple

bloom in Nova Scotia, Canada, increased from 10 to 18C, then declined, reaching a low intensity at 30C (Brittain, 1933). However, according to Morse (1975), bee activity occurs from 15 to 18C, but is maximum at 21C or higher.

The effects of temperature during or following bloom on fruit set of apple are somewhat controversial. Lapins and Arndt (1974), working in British Columbia, Canada, observed that fruit set in 'Delicious' was higher in warm than in cool areas. They concluded that warm temperatures during the 6 day period following full bloom favored fruit set. Forshey (1976) also considered that warm temperatures associated with sunny days following bloom of 'Delicious' were beneficial to fruit set. On the other hand, Lu and Roberts (1952) held apple trees of 'Delicious', 'Wealthy', and 'McIntosh' under controlled temperature conditions, and observed that fruit set was higher under low (13C) than under high temperatures (21 and 24C). When potted trees of 'Lired', 'Lobo' and 'Golden Delicious' were maintained for 2 weeks at several constant temperatures beginning with 0, 2, 3, or 5 weeks after full bloom, set was better at 10C than at either 15 or 20C (Grauslund and Hansen 1975). 'Cox's Orange Pippin' (henceforth referred to as 'Cox') accounts for more than 50% of fresh market apple sales in England, but year-to-year variation in yield is a major problem (Jackson and Hamer, 1980). Beattie and Folley (1978), in studying yield variation in 'Cox' from 1949 to 1975, found a significant negative correlation between yield vs. mean

maximum temperature during February, March and April (hereafter referred to as mtFMA), and significant positive correlation between yield and June temperatures. Jackson and Hamer (1980) hypothesized that in the years with higher mtFMA, the bloom was earlier, so the fruit set could have been decreased in two different ways: first, frost is more likely to occur in early than in late spring, so more frost damage to flowers and fruitlets could have occurred during warm springs; second, the temperature tends to be lower early in the spring, and cold temperatures negatively affect both bee activity and pollen tube growth. Therefore the conditions for pollination and fertilization were poorer in years with earlier bloom. Jackson and Hamer (1980) also found that daily mtFMA was negatively correlated with the number of air frosts but not the number of ground frosts, in April and May. Date of full bloom was positively correlated with the number of ground frosts in April and May, but not with the number of air frosts; neither daily mtFMA nor date of full bloom was significantly correlated with time to complete pollen-tube growth after the full bloom; and daily mtFMA was positively correlated with mean maximum temperature in "June", whereas date of full bloom was not. Jackson and Hamer (1980) concluded that the postulated detrimental effect of frost damage in years with higher mtFMA was not valid, since in the years when 'Cox' bloom was earlier, the number of ground and air frosts in April and May were below average and the number in June higher than

average. This statement by the authors may be inappropriate, since severity of frosts is often more important than number of frosts. However, multiple regression calculated by using mtFMA, daily maximum June temperatures, and calculated time of pollen-tube growth, gave equations which could explain the variations of 'Cox' yields from 1949 to 1975 (Jackson and Hamer, 1980).

To test the hypothesis that pre-bloom temperatures did indeed affect set, potted trees of 'Cox'/M.9 were placed under 3 different temperature regimes: control (out-ofdoors); 10C (warm); or 5C (cold) during February, March and April, and hand pollinated with 'James Grieve' pollen. Fruit set was higher in trees kept at 5C than in all other treatments, but 10C or 15C did not improve set (Jackson et al., 1982 b; 1982 c). Date of full bloom was delayed for 11 days by the 5C treatment compared to that of control trees, while holding trees at 10C advanced full bloom 1 day. The time required for pollen-tubes to reach the base of the style was 2 days for control and 10C trees vs. 6 days for the 5C trees.

Mist irrigation for evaporative cooling was applied to 'Cox' trees in the orchard for different periods. Misting began February 13 for all treatments and was discontinued April 15, April 22, April 27, or May 6. Water was applied whenever the temperature rose above 4.5C. All treatments delayed bloom 5 to 7 days in comparison with control trees, while time of pollen tube growth was delayed for 2 to 3

days. Misting increased fruit set (p < 0.001) regardless of timing (Jackson et al., 1982 b).

Records of fruit set for 'Cox', based upon crosses made at the East Malling Research Station from 1965 to 1979 (except 1977, when a frost occurred), pollen-tube growth (based on post bloom temperatures), and mtFMA were used for regression analysis (Jackson et al., 1982 c). The equations obtained for fruit set vs. pollen-tube growth, fruit set vs. mtFMA, and fruit set vs. mtFMA vs. pollen-tube growth were all significant. Although no mention was made as to cultivars used as pollen parents, compatibility between pollen parent and 'Cox', differences if any in rate of pollen tube growth, pollen viability, etc., the results obtained supported previous results obtained by Abbott (1971) in 'Lord Lambourne'. The results also indicated that a) female fertility is involved, since pollen from the same source was applied, b) fruit set varied as a function of temperature and c) low temperature pre-bloom can improve set even when post-pollination conditions are unfavorable (Jackson et al., 1982 c).

Effects of night temperatures were studied in potted trees of 'Cox'/M.106 (Jackson et al., 1982 d). Different periods of "warm" night temperatures were applied during March, April and May. Trees under warm night conditions bloomed earlier and set less fruit than did control trees. The authors concluded that the warm temperatures may stimulate metabolic activity during March and April. In a

similar experiment Jackson et al. (1983) analyzed buds and flowers for carbohydrate content at different stages of development. Tissues of trees held under warm night temperatures had lower water soluble sugars and polysaccharides than did those of control trees. Effects on fruit set were variable, but the authors suggested that a reduced level of carbohydrates might be responsible for the detrimental effect of high spring temperature.

Lakso (1984) compared apple yields in New York State over 15 years with mean maximum temperatures recorded from February 1 to April 15. Temperature differences explained 80% of the yearly variations in yield, with cool temperatures favoring yield.

To determine the mechanism of effects of pre-bloom temperatures on fruit set of apple, 'Cox' trees were held under controlled temperatures inside greenhouses (Miller et al., 1984). Flowers that developed under high temperature conditions were smaller, and spur leaves were thinner and smaller and had lower chlorophyll content than did controls. Fruit set under warm conditions was similar to that of control trees when pollinated immediately after opening, but became progressively poorer than that of controls as pollination was delayed. The duration of the period of flower fertility was shorter at warm temperatures, and longer at cool temperature, than that of flowers on control trees. Unfortunately the authors did not mention the temperatures for the different conditions. Frost

sensitivity of flowers at the green calyx stage was increased in trees held at higher temperatures.

Light intensity. Light may affect fruit set of apple in two ways: directly by influencing flower and fruitlet development, and indirectly by affecting bee activity. Brittain (1933) observed that bee activity was correlated with light intensity, especially the intensity of ultraviolet light. Hedrick (1908) reported that good crops of apples were associated with sunny days and warm weather during bloom. On the other hand, Boyd and Latimer (1933) noted that hand pollinated flowers of 'McIntosh' set more fruit under cloudy days with mild temperature than under sunny days with warm temperature (above 27C). Lakso (1984) shaded trees for various periods of time. Twenty or forty percent of full sun for only 2 days caused 92% fruitlet drop of 'Delicious' trees on dwarfing rootstock, even though the treatment was applied 4 weeks after bloom. Holding young apple trees under an 8-hour photoperiod for 2 seasons reduced shoot growth and caused abscission of all fruitlets in the "June" drop the second year although flower bud formation was hardly affected (Berüter, 1985 b). Fruit set of 'Delicious' apple trees was positively correlated with solar radiation during the 3 weeks preceding bloom (Dennis, 1981 c). Increasing the light intensity increased fruit set in 'Delicious' trees only slightly, while shading decreased it (Doud and Ferree, 1980). According to Cain (1972) apple and other tree fruits use only about 30% of the natural

light available in the north temperate zone for photosynthesis under natural conditions.

Artificial shade and defoliation have been used to study the importance of light on fruit trees. Rom and Ferree (1984) used potted 'Delicious'/M.106 to test the effects of both shading (55% shade = 45% full sunlight), and supplemental light (lamps placed 1.5 m above top of trees with a reflective plastic underneath the canopy), on fruit set. Shading from bud break to petal fall delayed bloom and decreased fruit set, but supplemental light had no effect. Because the trees were held in a greenhouse, light intensity on the controls was reduced to about 35% of full sunlight. Therefore 55% shade (45% full sun) was actually 16 to 30% full sunlight and supplementary light was actually 65% full sunlight (Rom and Ferree, 1984).

'Golden Delicious'/M.2 apple trees that were defruited 2 weeks after full bloom and shaded (53% full sun) during the growing season had lower fruit set next year than trees that were also defruited but not shaded (Hennerty and Forshey, 1972). These results showed that shade had a carryover effect on the next year's set. Both 30% and 73% shade applied to individual limbs of adult Starkrimson 'Delicious' trees from petal fall to 16 days after petal fall reduced both initial and final fruit set, but did not increase the thinning action of 400 ppm ethephon plus 1200 ppm carbaryl; 73% shade from 17 to 35 days after petal fall increased fruitlet drop and decreased final set in limbs

treated with ethephon/carbaryl (Lehman et al., 1987). Doud and Ferree (1980) also observed that shade previous to "June" drop decreased final set of 'Delicious' trees.

"June" drop can be extended and fruitlet abscission increased if shading is prolonged. Shade (37% full sun) from petal fall to 40 days after petal fall reduced fruit set of Redspur 'Delicious'/M.7 trees by 50% (Rom and Barritt, 1989). Timing of shading may be critical. Byers et al. (1985) observed that fruit set of Starkrimson 'Delicious'/M.7 was reduced by shading limbs (8% of FS) between 16 and 26 days after full bloom (DAFB), whereas shading for 10 day periods before or after this time had no significant effect. In contrast, shading (8% of FS) from 5 to 15; 10 to 20; 15 to 25; or 25 to 35 DAFB reduced fruit set of limbs of 'Stayman'/M.111. In Redchief 'Delicious'/M.111 the same shade intensity applied to entire trees for 10 day periods starting at 18, 23, or 28 DAFB caused abscission of all fruitlets (Polomski et al., 1988).

However, shading (92%) for a period of 4 days only (17 to 21 DAFB) of entire trees of Redchief 'Delicious'/M.111 reduced fruit set by 50% relative to control trees (Byers et al., 1990 a). The same treatment plus a spray of 900 ppm carbaryl 50 WP, increased fruit drop to 89%, while carbaryl alone removed only 25% of the fruitlets. Shade (92%) was applied to entire trees of Redchief 'Delicious'/M.111 for 10 day periods beginning at 5 day intervals from 5 to 47 DAFB (Byers et al., 1990 b). Shading during all periods except

47 to 57 DAFB significantly increased fruitlet abscission relative to that of control trees. However, shading from 5 to 15 DAFB caused less fruit drop than did shade treatments beginning 10 to 25 DAFB. Shade treatments that started at 30 days and later caused progressively less fruit abscission. The same shading intensity (92%) applied to entire trees of Redchief 'Delicious'/M.111 for shorter periods (3, 5, or 7 days) from 13 to 33 DAFB also significantly reduced fruit set. The period of greatest sensitivity of fruitlets to shade treatment was 10 to 30 DAFB (Byers et al., 1990 a, b).

Rain. Information about direct effects of rain on pollinated flowers is contradictory. Hedrick (1908) reported that in a period of 25 years, fruit set was negatively correlated with wet weather, and suggested that rain washed off the stigmatic secretion, as well as pollen grains from anthers, and caused bursting of pollen grains. However, Boyd and Latimer (1933) observed that the number of pollen grains removed by heavy rain did not appreciably limit fruit set, and Beattie and Folley (1977) reported that rain during bloom was not a significant factor in variations of yield of 'Cox'.

Wind. Pollen grains of apple are heavy and sticky, and wind does not play a significant role in pollen transfer; therefore apple is dependent upon insects for crosspollination (Free, 1964). However, wind can affect fruit set indirectly by limiting bee flight. Brittain (1933)

observed that wind speeds higher than 3 miles per hour caused a progressive decrease in bee activity.

2. Effects of plant characteristics.

Cultivar and strain. The process of fruit setting in fruit trees is a complex multi-dimensional phenomenon under both genetic and environmental control (Chaplin and Westwood, 1980). Differences in setting ability among apple cultivars and strains is well documented. In Ohio, 'Delicious' trees in mixed plantings with other cultivars showed a tendency to set light crops (Howlett 1928). Childers (1969) suggested that the use of better strains together with better cultural practices and fungicides could improve yields. Dennis (1979) reviewed the literature on apple yield and concluded that 'Delicious' had lower yield than 'Jonathan', 'McIntosh', 'Northern Spy', 'Golden Delicious', 'Winesap' and 'Rome Beauty'. Using yield records for 'Delicious', 'Jonathan', 'McIntosh' and 'Northern Spy' at the Graham Experiment Station, Grand Rapids, MI, from 1949 to 1970, he observed that 'Delicious' and 'Northern Spy' yielded less per tree than 'Jonathan' and 'McIntosh'. When the yield was expressed per cm^2 of the trunk cross-sectional area, 'Jonathan' and 'McIntosh' still produced more than 'Delicious', while 'Northern Spy' was least productive. Rahemi (1981) observed no significant differences in final set of 'McIntosh' and 'Red Prince

Delicious' in E. Lansing, MI, in 1980, although initial set was higher in 'McIntosh'. However, in another experiment conducted at Leslie, MI, in 1991, 'McIntosh' trees had higher initial and final fruit set than did Starkrimson 'Delicious'.

Strain of Delicious can also affect yield. Westwood et al. (1967) reported that the fruit set of four sports of 'Delicious' varied significantly, even with the same flower density. Idaho Spur had the highest set, Starking the lowest, with Starkrimson and Chelan Red intermediate. Differences in setting ability between strains of 'Delicious' have also been reported in Michigan (Dennis, 1981 a, 1988). Data on several 'Delicious' strains recorded in two states in the USA, and in Italy and Poland were summarized by Dennis (1979). He observed that differences in yield occurred in all locations, but that the greatest variation was observed in Ohio and Italy. However, information on flower density and rootstock could also have influenced productivity. The reasons for cultivar and strain differences in setting ability are not well known. However, factors include availability of compatible pollen, presence of sufficient numbers of bees and favorable weather conditions.

Since all apple cultivars present some degree of selfincompatibility (Janick and Moore, 1975), and development of parthenocarpic fruit in commercial orchards is a rare event (Dennis, 1985) cross-pollination is necessary in commercial

apple production. Cultivars such as 'Golden Delicious', 'Jonathan' and 'Rome Beauty', considered self-fruitful, do not produce more than 25 to 50% of their potential unless pollinator trees are provided (Murneek, 1937). Way (1978) observed that 'York Imperial', 'Golden Delicious' and 'Rome Beauty' are self-fruitful; however, cross-pollination increased their crop. Pollinizer trees have to be of diploid cultivars (2n = 34 chromosomes), whereas triploid cultivars (51 chromosomes) are of no value as pollinizers, since they produce pollen of low germination capability (Dennis, 1985; Overholser and Overley, 1931; Wellington, 1947). The pollinizer trees must produce large amounts of viable pollen that is compatible with the recipient cultivar (Dennis, 1985; Wellington, 1947). The amount of pollen received per stigma during cross-pollination may increase fruit set. Williams (1970) observed that supplemental hand pollination increased fruit set of 'Cox' in most of the 21 orchards studied in England. Forshey (1978) considered that in 'Delicious' the stigma should be saturated with pollen, since a very low proportion of pollen tubes grow enough to reach the embryo sac. Visser and Verhaegh (1980) suggested that the presence of pollen grains can stimulate pollen tube growth. They pollinated 'Golden Delicious' flowers twice in periods of 24 to 48 hours, using pollen of scab-resistant parents, which allowed them to identify the male parents by screening the plants originated from the seeds. They determined that a higher percentage of seeds originated from

the second pollination (63%) than from the first (37%). They concluded that the pollen grains from the first pollination that partially penetrate the styles favored penetration of pollen tubes from the second pollination, and increased their growth rate. However, the effect of doublepollination may be cultivar-dependent. Rahemi (1981) reported that supplemental hand pollination significantly increased fruit set of Starking 'Delicious', but not of 'McIntosh'.

Flower characteristics. Anatomical differences may be responsible for differences in fruit set among apple cultivars. Roberts (1945; 1947) reported that bees can extract nectar of 'Delicious' flowers without transferring pollen to the stigmas. Robinson (1980) reported that in 'Delicious' there are basal gaps between stamens which permit bees to collect the nectar by sideworking the flower. He studied the width of basal gaps in several apple cultivars and observed that in 7 strains of 'Delicious' these gaps were wider than in 11 other apple cultivars.

Ovule longevity is also an important factor in apple fruit set. Hough 1947 studied causes of differences in fruitfulness between 'Arkansas Delicious' and 'Grimes Golden' and observed that two problems frequently occurred in 'Delicious': tardy initiation of the megaspore mother cell, and slower rate of development of megaspore and embryo, as compared to that of 'Grimes Golden'. Embryo sacs with tardy initiation and low rate of development very

seldom differentiate to eight nucleate embryo sacs in time for fertilization. He also observed that some apparently normal embryo sacs broke down after flower opening, even though the flower was already pollinated with compatible pollen. Similar problems of delayed development and early degeneration of the embryo sac of 'Delicious' were also observed by Hartman and Howlett (1954). They observed that many ovules had already started to degenerate at anthesis, while a higher percentage of ovule degeneration was observed at 72 hours after anthesis. At 48 hours after anthesis ovule degeneration had reached 30%. Williams (1965) found a similar relationship between ovule degeneration and fruit set of 'Cox' in England. He coined the term "effective pollination period" (EPP) for the period during which pollination of a flower results in fertilization. This period is a function of ovule longevity and pollen tube growth, varies with cultivar and year, and is the main factor in fruit setting. EPP varied from 2 to 10 days after anthesis depending on cultivar (Williams, 1965).

Bud size. Flower bud size may influence fruit set of apple; however, discrepancies among results have occurred. Treccani et al. (1982) classified dormant flower buds of 'Yellow Spur' on M.106 apple trees into 3 categories: 2.5 -3.5; 4.0 - 5.0; and 5.5 - 6.5 mm diameter. They observed three main peaks of fruitlet abscission, the first between May 10 and 24, the second between May 25 and June 4, and the third between June 5 and 20. The second and third peaks of

fruitlet abscission were most marked in fruitlets derived from small buds. Positive correlations were found between bud size and chemical content (sugar, nitrogen, amides, and calcium) of the buds of first and second year growth. Bud size and chemical content were both correlated with spur growth, lateral shoot size, number and size of flowers, and fruit set. Buszard (1983) measured flower buds of 'Cox' on M.9 apple trees that were defruited and, in a second comparison, trees that produced a heavy crop in the previous growth season. Defruited trees had flowers with significantly larger receptacle diameters (3.3 mm) than did heavily cropped trees (2.7 mm). Although the defruited trees had a higher number of fruit/tree and fruit/ cm^2 of the trunk cross section area, fruit set as a percent of flowers was higher in heavily cropped trees than in defruited trees. Defruited trees had more than twice as many flowers as did heavily cropped trees, therefore flower density was probably more important than flower bud size. Blasberg (1943) grouped dormant flower buds of 'McIntosh' apple trees into the following groups ≤ 3.5 , 3.6 - 4.0, 4.1 to 4.5, and > 4.6mm diameter. He observed that the number of fruit per 100 flower clusters was higher in the larger buds. The following year, however, the same trend was not observed, and flower density was the prevalent factor in fruit set, rather than flower bud size.

<u>Rootstock</u>. Rootstock is another factor that can influence fruit set of apple. Dennis (1979) summarized data

of several authors in Germany, Poland, Rumania, and two states of the U.S.A on the influence of rootstock on yield of 'Delicious' apple. In Rumania, differences between rootstocks were small (25% at most), while in Poland, trees on 'Alnarp 2' had higher yield efficiency than those on 'Antonovka' seedling. Trees on M.9 and M.26 bore similar crops. In Ohio, cropping of trees on seedling or on M.16 was roughly half that of trees on M.2. In New York, trees on M.13 or on seedling produced less than 50% of the yield of trees on M.2. Carlson and Tukey (1959) observed yield of 'McIntosh', 'Cortland', 'Fameuse', 'Golden Delicious', 'Northern Spy', and 'Wealthy' on East Malling rootstocks in Michigan. Unfortunately, only 'McIntosh' and 'Cortland' trees were grafted on all 6 rootstocks (M.2, M.4, M.5, M.7, M.12, and M.13). Nevertheless, precocity varied inversely with rootstock vigor. Neither rootstock nor cultivar alone determined productivity, but interaction was evident between the two. Dennis (1981, b) observed the fruit set of 'Red Prince Delicious' on eight MAC (Carlson, 1978) rootstocks over 3 seasons in Michigan. He concluded that trees on MAC 9 had higher fruit set, both on a per cluster basis and when expressed in number of fruits per cm limb circumference, than did trees on any other rootstock clones (MACs 1, 4, 5, 11, 16, 24, and 30). Dennis (1981 c) analyzed data of 'Delicious' yield obtained in more than 30 locations, mainly in the United States and Canada. He concluded that both rootstock and strain can have a marked effect on fruit set
of 'Delicious'. Starkspur Supreme 'Delicious' trees on 9 rootstocks were planted at 27 locations in the United States and Canada. Trees on MAC 9 were more precocious and had higher yield efficiency than those on any of the other rootstocks, although trunk cross-sectional area was similar to that of M.9 and of M.9 EMLA (NC-140, 1987).

Both Blasco et al. (1982) and Jackson et al. (1982 a) treated 'Cox' apple trees on M.9, M.26, M.7, and M.106 with hormone mixtures (GA₃ + diphenylurea + an auxin) at petal fall. Both initial and final set were increased on trees on M.9, while only initial set was increased in trees on the other rootstocks. Non-treated control trees on M.9 also retained more fruits with few seeds than trees on more vigorous rootstocks. The authors suggested that the fruitsetting hormone spray caused retention of a larger proportion of few-seeded or seedless fruitlets, but that only trees on M.9 could retain these fruitlets to maturity (Blasco et al., 1982; Jackson et al., 1982 a). Schechter et al. (1991), studied the effect of rootstock on canopy development, photosynthesis and yield of Starkspur Supreme 'Delicious' in Ontario, Canada, using trees planted in 1980 (NC-140, 1987). They observed that shoot leaf photosynthesis (PN) was significantly higher in trees on M.7 EMLA and on MAC 24 than in trees on M.26 EMLA, OAR 1, Ottawa 3, M.9 EMLA, M.9, MAC 9, or M.27 EMLA. Unfortunately the PN measurements were made after August 30, therefore the data cannot be related to fruit set. These authors also found

that PN rate was higher in shoot leaves than in spur leaves, and that leaves on fruiting spurs had significantly higher PN rates than those on non-fruiting spurs regardless of rootstock used (M.26 EMLA and OAR 1 only). Again, the data cannot be related with fruit set, since the earliest PN measurements were made in July 18. Fisheye photography showed that yield was positively correlated with percent of sky covered by the tree canopy (r = 0.80). According to the authors, yield per tree was a function of sky coverage by tree canopy; thus M.24 (most vigorous rootstock) had the highest fruit yield per tree, followed by M.7 EMLA and M.26 EMLA. Neither M.26 EMLA nor OAR 1 affected PN rate of the scion, thus the hypothesis of Schechter et al. (1991) that yield efficiency on these two rootstocks was related to photosynthetic efficiency is not valid. When their data are converted to yield in kg per cm^2 trunk cross-sectional area, the relative productivity changes dramatically. Yields as a percentage of that of MAC 24 were 94, 121, 132, 138, 163, 180, 191, and 192 for OAR 1, M.27 EMLA, M.7 EMLA, MAC 9, M.6 EMLA, Ottawa 3, M.9, and M.9 EMLA, respectively. Thus only trees on OAR 1 yielded less than those on M.24, all other rootstocks increasing yield efficiency by 20 to 90%. Therefore, trees on more dwarfing rootstocks, even though they had lower photosynthetic activity, diverted more photoassimilates to fruit production than the more vigorous trees on MAC 24. Another report on this project (NC-140, 1987), containing data from 27 sites in the United States

and Canada, also indicates that yield efficiency was higher on M.9, and that trees on MAC 24 and on OAR 1 were delayed in production.

Rootstock can influence ovule longevity of some apple cultivars. Embryo sac degeneration at petal fall was greater in 'Delicious' trees on seedling rootstock than in trees on M.9 (Marro, 1976). When flowers of 'Granny Smith' and of 'Granny Smith' spur clone on both seedling and M.9 rootstock were collected at balloon stage, the embryo sac persisted longer in both cultivars on M.9 than on seedling rootstock (Cobianchi et al., 1978). The greatest number of receptive ovules was found at full bloom, regardless of cultivar and rootstock.

Interstem. Interstems of dwarfing rootstocks can also affect scion size and productivity, even with a vigorous root system (Carlson and Oh, 1975; Cummins, 1971, 1974 a, 1974 b). The percentage of fruit set of six-year-old 'Cox' trees was greater on M.9 EMLA than on M.111 (EMLA), but set was intermediate in trees that had a 15 cm M.9 EMLA interstem grafted on a M.111 rootstock (Webster et al., 1983). Trees of Red Prince 'Delicious'/M.8/Alnarp 2 yielded about 5 times as much fruit as did trees with a seedling interstem (Carlson and Oh, 1975). 'Jonathan' and 'Red Delicious' scions were grafted on 10, 20, and 30 cm M.8 interstem on Alnarp-2 rootstock, and compared with the same cultivars on seedling rootstocks. After 10 years of observation, tree size was inversely related to length of

interstem. Productivity, adjusted for tree size, was approximately 2, 3, and 4 times higher using M.8 interstems 10, 20, or 30 cm long, respectively, in comparison with seedling stocks (Carlson, 1974).

3. Effects of cultural practices.

Pruning and training. Pruning and training may affect fruit set of apple; however, their effects are probably indirect through influencing light conditions inside the tree canopy. Batjer (1962) observed that lightly pruned 'Delicious' apple trees had higher yields due to higher numbers of flowers produced in comparison with heavily pruned trees, but fruit set was not affected. Four apple cultivars on both 'Antonovka' seedlings and M.7 rootstock that were either pruned by tipping or shoot thinning during the dormant period had fewer flowers and lower set and yield than unpruned control trees (Mika, 1974). The author suggested that winter tipping disrupted the natural correlation between the buds and caused formation of long shoots. Pruning also reduces the foliar area of the tree, lessens the amount of stored nutrients and reduces the size of the whole tree and the number of fruit buds. Although the author did not refer to shoot-fruit competition, tipping dormant branches every year may increase shoot-fruit competition. Taylor and Ferree (1984) observed that summer pruning did not affect fruit set the next year; however,

thinning response to NAA was significantly lower on trees that had been summer pruned for 2 years in succession than in control trees. In most of the literature on pruning, little attention is paid to its effects on fruit set, more attention being given to flowering and fruit quality. However, in shaded areas of the canopy, light intensity may be 16% FS (Cain, 1971) or less (Heinicke, 1966), and these low levels may limit fruit set (Flore, 1980; Heinicke, 1963, 1966; Jackson, 1970).

Nutrition. Nutrition may also influence fruit set of apple. Chaplin and Westwood (1980) suggested that all sixteen mineral nutrients generally accepted as essential to higher plants may affect fruit set. By definition, essential means that the plant cannot complete its life cycle in the absence of the element. Since fruit set is part of this cycle, it may be affected by a deficiency of any of these essential mineral. Stainer (1986) reported that urea sprays (3 kg/ha) increased the yield of 'Golden Delicious'/M.9 apple trees by 8% the year following treatment. Shim et al. (1980) observed that apple trees sprayed with urea after harvest had greater shoot growth and fruit set than either control trees or trees that received urea by soil application. Williams (1965) and Hill-Cottingham and Williams (1967) applied nitrogen to apple trees in late summer, and observed an increase in fruit set in the next spring. They suggested that late summer nitrogen increases ovule longevity, and consequently

prolongs the effective pollination period (EPP). Taylor and Goubran (1975) observed that in 'Jonathan' apple trees deficient in phosphorous (P), bud break was delayed and the number of flower and vegetative meristems were reduced. The delayed bloom caused the trees to bloom later than pollinizer trees, reducing cross-pollination and consequently fruit set.

Potassium (K) is not known to affect fruit set (Chaplin and Westwood, 1980). These authors reported that Vang-Petersen (1975) applied two sprays of KNO3 just before bloom but no effects on fruit set, number of fruit per tree, or fruit size were observed. Boron (B) deficiency in higher plants causes death of meristematic points, particularly flowers (Chaplin and Westwood, 1980). The authors stated that apparently B plays an important role in fruit set. B application can increase fruit set of several species, such as pear (Batjer and Thompson, 1949; Degman, 1953; Johnson et al., 1954), plum (Chaplin et al., 1977), and cherry (Chaplin, 1977), unpublished data (cited by Chaplin and Westwood, 1980). In apple, two B sprays early in the growing season increased fruit set of 'Stayman' but not of 'Jonathan' or 'Golden Delicious' (Bramlage and Thompson, 1961). Davidson (1971) observed little increase in 8 of 11 experiments on apple in New Zealand using B sprays at open cluster and petal fall; in only two cases was the increase significant.

Zinc (Zn) may affect fruit set through influencing auxin synthesis (Chaplin and Westwood, 1980). They reported positive effects of Zn application in grapes (Khanduja et al., 1974), and plum (MacSwan, 1970). Davidson (1971) in New Zealand obtained little effect with Zn application in apple. Manganese and molybdenum also had little effect, while iron application gave small but significant increases in set of apple.

Fungicides. Fungicide sprays during bloom can decrease fruit set of apple, both by repelling bees and by inhibiting pollen germination and pollen tube growth, although results are sometimes contradictory. Church and Williams (1977) observed that pollen tube growth was inhibited by fungicides in vitro; however, none of the fungicides tested decreased fruit set in the orchard. On the other hand, Captan significantly reduced pollen germination <u>in vitro</u>. Stainer (1986) observed that Dicofap (40% captan + 10% folpet + 5% captafol), captan, and mancozeb considerably reduced pollen germination. Bees were repelled for 24 hours by captan and nuarimol, which reduced fruit set by 60% and 42%, respectively. However, Bayleton (triadimefon) had no effect on either pollen germination or bee visitation.

Hormone treatment. Parthenocarpy in apple can be induced by both GA_3 and GA_4 (Bukovac, 1963). However, Dennis and Edgerton (1966) applied GA_3 and its butylcellosolve ester at concentrations of 100, 250 and 500 ppm to open pollinated flowers on apple trees of 5

cultivars, and there were no significant increases in fruit set; on the contrary, in some cases set was decreased by the treatments. Greene (1986) reported that post-bloom application of GA_{4+7} (50 to 150 ppm) increased fruit set of 'Empire' and 'McIntosh' apple trees, and that the treatments decreased number of seeds per fruit, while fruit size was not affected. Synthetic auxins (e.g., NAA, NAAm) and ethephon (ethylene generator) can reduce set of apple (Chaplin and Westwood, 1980; Dennis, 1979). Fruit set of apple can be increased by plant growth retardants such as daminozide (Batjer et al., 1964), TIBA, triiodobenzoic acid (Bukovac, 1968), and paclobutrazol (Tymoszuk and Mika, 1986). Aminoethoxyvinylglycine (AVG), an ethylene synthesis inhibitor, also increased fruit set of apple (Dennis et al., 1983; Rahemi, 1981; Walsh and Faust, 1982). Two applications of N-phenylphthalamic acid to flowering Starkrimson 'Delicious' and Starking 'Delicious' increased fruit set of both strains (Bork and Teleky, 1983). Combinations of growth regulators have also been used. GA_{4+7} at 10% plus daminozide at 0.15% applied to apple trees once at full bloom was twice as effective as 4 applications of GA_{4+7} alone during and following bloom (Joosse, 1982). A mixture of three growth regulators kinetin [or N,N'diphenylurea (DPU)], 2-naphthoxyacetic acid (NOXA), and gibberellic acid (GA₃), increased fruit set of 'Cox' apple trees (Kotob and Schwabe, 1971, Buszard, 1983). Sprays of the polyamines spermine, spermidine and putrescine at 9 days

after full bloom increased fruit set of open pollinated apple trees of 'Ruby Spur' (Costa and Bagni, 1983). Concentrations of 10^{-4} and 10^{-5} M substantially increased fruit set and yield per tree.

Girdling or scoring. Trunk or branch girdling (ringing) or scoring can stimulate fruit set in fruit trees. Girdling young 'Delicious' apple trees increased fruit set 68 to 116% in 2 successive years (Batjer, 1961). Batjer and Westwood (1963) used a factorial arrangement of treatments with young Starking 'Delicious' apple trees (no pruning vs. moderate pruning; two levels of nitrogen; scored vs. not scored). The trees were scored in both 1959 and 1960 at 10 to 14 DAFB. In 1959, scoring increased fruit set regardless of pruning intensity or N level, while in 1960 scoring reduced set in low N trees, but increased it in high N trees. Although scoring stimulated flowering in both 1960 and 1961, it reduced bloom in moderately pruned, high N trees in 1962. Unpruned trees that were both heavily fertilized and scored had the highest cumulative yield per ha over the three years (Westwood, 1978). Scoring of the trunk of 5-year-old 'Delicious' apple trees at either 7 or 25 DAFB increased yield during the year of girdling (Burkhart and Westwood, 1964), the earlier treatment being more effective. Scoring also increased bloom the following year. Scoring in two consecutive years increased yield in both years, but reduced growth. Hansen (1981) observed that either ringing (2 mm of bark removed) or scoring at bloom or

at two weeks after bloom increased fruit set of 'Cox' on both M.26 and M.104, and of 'Golden Delicious' on M.9. Williams (1985) girdled trees of 'Discovery' on M.106 at the beginning of their 6th growth season (April, 1982) by taking a 10 mm wide ring of bark at 15 - 20 cm above the graft union. The ringing treatment was repeated in both 1983 and 1984. The accumulated yield of the girdled trees was 2093 boxes per acre vs. 1783 boxes for control trees. Tree size was reduced and bloom density was increased in 1983. Buszard (1983) girdled limbs of 28-year-old 'Cox' on M.9 at "pink" bud stage by taking a 1 cm wide ring of bark at the base of the limbs. Girdling stimulated fruit set as well as increasing response to the "Wye mixture". Although most reports indicate positive responses to girdling, Rahemi (1981) obtained no response to double scoring of 'McIntosh', 'Golden Delicious' and 'Red Prince Delicious' limbs 18 DAFB. The author suggested that scoring was done too late to affect fruit set. Dennis and Edgerton (1966) scored limbs of 'Wealthy' bearing emasculated flowers and observed a highly significant effect (p < 0.01) of scoring on fruit set of seedless fruits after "June" drop. The effect was independent of GA treatment.

B. The Role of Carbohydrates in Fruit Set

Loescher et al. (1990) considered reserves in woody plants to be important for winter survival, respiration, development, and growth of buds during the dormant period, as well as for flowering. All perennial organs of a woody plant may store carbohydrates, but roots usually contain the highest concentrations; sugars can be used as reserves, but starch is usually the main reserve form in the aerial parts (Loescher et al., 1990).

1. <u>Main carbohydrates in apple and their seasonal</u> <u>levels</u>.

Starch. Kraybill et al. (1925) observed that starch levels from June to September were lower in fruiting than in non- fruiting spurs of 'Baldwin' apple. Grochowska (1973) measured levels of starch in bearing and non-bearing spurs of mature 'Landsberger Reinette' apple trees over a 4-year period. Each year starch content of bearing spurs fell dramatically relative to that of non-bearing spurs, and was consistently lower in the former during the 5th and 6th week after full bloom. Differences in starch content became statistically significant about 3 weeks after full bloom.

Raese et al. (1977) measured sorbitol, sucrose, glucose, fructose, and starch levels in sap and wood samples of 2-year-old branches of mature 'Red Delicious' apple trees

at different times during the dormant period, as well as in excised branches kept at different temperatures. On all sampling dates (October 29, November 14, and January 8), starch content was at least 2 to 3 times as high as the content of total soluble sugars, regardless of temperature treatment. In January, levels of sorbitol and all sugars increased, while starch content decreased, the most rapid change occurring at temperatures below -0.6C.

Schimpf and Stosser (1984) measured seasonal starch accumulation in terminal shoots of 'Boskoop' and 'Mutsu' apple trees during an entire year. Starch declined with decreasing temperatures in the early winter, and was almost completely hydrolyzed by February. Starch began to appear again in early April, but decreased again with bud swell, reaching a minimum at full bloom.

Stassen (1984) studied the seasonal variation of carbohydrates in 2-year-old 'Golden Delicious' apple trees. Starch content began to decline several weeks before, and continued for several weeks after, bud break. He concluded that starch is an important compound for reserve energy as well as a carbon source for bud development and initial spring growth.

Sorbitol and sugars. Sorbitol is the major soluble carbohydrate in Rosaceous plants and has an important function in the translocation of photosynthate (Yamaki, 1984). It is formed by reduction of glucose, fructose, and sorbose, and is the main radioactive compound formed from

¹⁴CO₂ during photosynthesis in numerous species (Bieleski, 1977). Apple contains sorbitol (Plouvier, 1963; Wallaart, 1980).

Whetter and Taper (1963) quantified levels of sorbitol and what they called "related sugars" (sucrose, glucose and raffinose) in leaf buds or leaves of 'McIntosh' apple trees from April 4 to October 19. Sorbitol, sucrose and glucose were present at all times of sampling, while traces of raffinose were found in leaves only in April, September, and October. Sorbitol content of the leaves was higher than sucrose content at all sampling times. Although values for sucrose were higher than those for sorbitol in the leaf buds, the differences were not statistically significant. When growth began in leaf buds, sucrose level declined and glucose content increased dramatically. Sorbitol did not appear to be involved in metabolism prior to bud break. At bud burst, sorbitol, sucrose and glucose levels increased as the leaves expanded. Sorbitol also increased in the flower buds as the buds developed, whereas sucrose and glucose content declined. Whetter and Taper (1963) assumed that some interconversion of sorbitol and glucose occurred.

Williams and Raese (1974) extracted sap of 2-year-old branches of 'Red Delicious', and 'Golden Delicious' apple trees at 10 day intervals (1970, 1971), or 3 to 4 day intervals (1971, 1972) from harvest until the end of the dormant period. Levels of reducing sugars, sorbitol, and especially sucrose, in the tissues increased as the

temperature decreased in the fall, and decreased as temperature rose in the spring. They concluded that both sorbitol and sucrose are important storage carbohydrates during the dormant period. The study was continued for another year (Raese et al., 1977). When two-year-old branch pieces were held at controlled temperatures, sorbitol level in the sap increased when shoots were stored at -0.6C for one week. The authors suggested that sugars were being converted to sorbitol, because levels of fructose, glucose, and sucrose were less at -0.6C than at either 1.1C or -2.2C. They based this on the fact that both glucose and fructose are considered to be precursors of sorbitol (Bonner, 1952; Chong and Taper, 1971). They also suggested that an inducible enzyme of sorbitol synthesis might be triggered by sub- freezing temperatures (Neilands et al., 1958). Levels of glucose and fructose were higher in the wood at temperatures lower than -0.6C, whereas sorbitol level in the wood was less affected by temperature than sorbitol in the sap (Raese et al., 1977).

2. <u>Metabolism of carbohydrates in apple</u>.

Hansen (1971 b) applied ${}^{14}\text{CO}_2$ to buds, flower clusters, and fruits from green tip to after fruit set. He observed that flowers fixed a large amount of ${}^{14}\text{C}$ immediately prior to opening and that considerable radioactivity occurred in the petals. At bloom and thereafter, the loss of petals and

unfertilized flowers between exposure and sampling could explain the relatively low amounts of radioactivity in flowers or fruitlets. Rapidly growing fruitlets were very active in fixation of 14 C (about 60 to 90% more activity than leaves).

Bieleski (1977) studied the fate of $^{14}CO_2$ in apple leaves. Within minutes after application of $^{14}CO_2$, leaves had converted 58 to 80% of 14 C to sorbitol, 7 to 9% to sucrose, and from 1 to 4% to glucose. Yamaki (1980) demonstrated that a sorbitol oxidase in apple leaves converts sorbitol to glucose in the absence of NAD or NADP. Grant and Rees (1981) compared the roles of sorbitol and sucrose in seedlings of apple and followed the synthesis and breakdown of sorbitol in various tissues (root system, root apices, stem bark and wood, and leaves) both in darkness and in the light. They exposed the tissues to $^{14}CO_2$ in the light and applied ¹⁴C-fructose and ¹⁴C-sorbitol to excised parts of the seedlings. Sorbitol synthesis occurred only in the leaves, but was not dependent on photosynthesis. Sorbitol was metabolized in all tissues examined, but metabolism was intense only in the root apices and in leaves kept in darkness.

Loescher et al. (1982) studied the metabolism of sorbitol in young expanding apple leaves as they developed in the spring. Two days after the spur leaves reached 2.5 cm in length, they had become net exporters of photosynthates; export increased rapidly during the next 11

days. During this period, chlorophyll content and leaf length almost doubled, while carbohydrate content on a dry weight basis increased 3 times. Sorbitol was responsible for most of the increase (from 2.7 to 8.4%) while sucrose increased only slightly and glucose and fructose changed very little. Sorbitol synthesis did not occur until 7 days after leaves had reached 2.5 cm length (beginning of sampling); activity of aldose-6-phosphate reductase (A6PR) was not detected, while sorbitol dehydrogenase activity was high until 4 days, then decreased to a steady state at 7 days. On the other hand, A6PR activity increased from the 7th day, reaching a peak at the 16th day. The increase in photosynthesis and soluble carbohydrates was accompanied by increased synthesis and decreased oxidation of sorbitol. Berüter (1985 a) observed that sucrose was not detectable during the initial development of 'Golden Delicious' fruitlets, but accumulated steadily thereafter. Sorbitol, glucose, and fructose declined until two weeks before the start of "June" drop. Acid invertase activity decreased rapidly during the period when sucrose was absent. Sorbitol dehydrogenase, which catalyzes the transformation of sorbitol to sucrose, was absent in the pre-drop stage at a time when sorbitol content was relatively high. When sorbitol dehydrogenase appeared in sugar-accumulating fruitlets the concentration of sorbitol decreased while the fructose levels continued increasing until fruit development These results suggest that sucrose is the ceased.

predominant source of carbon for cellular growth in the young fruitlets, whereas during the sugar storage phase, sorbitol is converted to fructose. Fruitlet abscission during "June" drop was not related to the carbohydrate concentration of the fruit (Berüter, 1985 a).

3. Transport of carbohydrates.

Wareing and Patrick (1975) reviewed the factors related to carbon partitioning, based on source-sink relationships. Sources were defined as regions of production and sinks as regions of consumption of assimilates. Sources and sinks were characterized from the following three points of view: 1) in relation to direction of transport, sources exporting and sinks importing assimilates; 2) in relation to plant parts, source referring to mature leaves, the chief site of photosynthesis, and sinks to the organs (fruits, roots, and other storage organs) that import assimilates; and 3) in relation to metabolic activity, sources producing assimilates by photosynthesis or by mobilization of stored reserves, sinks utilizing assimilates in growth and respiration.

Daie (1985) reviewed carbohydrate partitioning and metabolism in plants. She stated that yield depends on two factors: first, the proportion of carbon available for export from the leaf (source), which varies with rates of carbon fixation and of phloem loading; second, the capacity

of storage organs to import carbon, which is a function of sink strength. Daie (1985) noted that carbon partitioning can be regulated at several sites within the plant: however. this regulation does not occur in isolation, for communication exists between source and sink. Such communication requires signal transmission, but the nature of such signals is unknown. One hypothesis is that sinkinduced reduction in turgor pressure at the source favors loading and movement toward sinks. Another hypothesis suggests that source-sink communication is controlled or coordinated by plant hormones (Daie, 1985). Daie (1985) emphasized that partitioning is clearly a function of the ability of the various parts to compete for assimilates. Although the role of plant hormones in regulating the translocation of photosynthates remains uncertain, they surely can regulate assimilate transport indirectly by stimulating growth.

Transport in apple. Webb and Burley (1962) applied ¹⁴C-sugars to terminal leaves of 2-year-old 'Golden Delicious' apple trees. Because sorbitol was translocated more readily than sucrose, they concluded that sorbitol was the principal carbohydrate transported in apple trees.

Williams et al. (1967) applied 14 C-sorbitol and 14 Csucrose to leaves of young 'Delicious' apple trees and observed that sorbitol was translocated at a much faster rate than was sucrose. 14 C-sorbitol applied to leaves of fruiting spurs was transported to fruits; however, little or

no sorbitol was transported from one fruit to others in the same cluster.

Hansen (1967) used $^{14}CO_2$ to study the effect of fruit on translocation and distribution of photosynthates in apple. About 90% of the 14 C absorbed by the leaves was transferred to nearby fruits, most of this within 5 days. The content of 14 C in the leaves fell more rapidly on branches with fruits than in those without fruits, and young expanding leaves retained more ¹⁴C than mature ones. Similar observations were made by Loescher et al. (1982) and Hansen (1971 b). In 'Golden Delicious' and 'Gravenstein' apple trees (Hansen, 1970 a), the majority of the $^{14}CO_2$ absorbed by leaves on fruiting spurs was transferred to the fruit on the same spur, and the total amount of 14 C in the system as a whole remained virtually constant over time. Declining levels of sorbitol and sucrose accounted for most of the loss of activity in the leaves. In a later study Hansen (1970 b) applied $^{14}CO_2$ to leaves on fruiting spurs; sorbitol was the primary substance translocated, although some sucrose was also exported.

Hansen (1982) stated that apple fruits are major sinks under most conditions. However, at the beginning of the growing season in well-established trees, and at all times in young trees, growing vegetative parts may be significant sinks. In defoliation experiments with 'Golden Delicious' and 'Gravenstein' apple trees, fruits were able to attract assimilates from leaves up to 1 m away, with no reduction in

size, provided the leaf/fruit ratio was maintained constant; as distance increased beyond 1 m, dry weight of the fruit decreased (Hansen, 1977).

Schumacher et al. (1987) defoliated 7-year-old trees of 'Gloster' on M.9 to give varying number of leaves per fruiting shoot. Leaves were removed at petal fall or 10, 20, or 30 days thereafter. Additional treatments included removal of none, 1/2, or all flowers from neighboring branches. Earlier and more severe defoliation markedly inhibited shoot growth and increased "June" drop. Later defoliation had little or no effect on shoot growth if neighboring branches had no fruit, and stimulated fruit drop only slightly. The authors explained these effects as reflecting transport of assimilates from non-fruiting to fruiting branches. Fruit growth after "June" drop was strongly inhibited by defoliation but was promoted by deflowering neighboring branches (Schumacher et al., 1987).

Loescher et al. (1982) concluded from their studies (see Metabolism section above) that expanding apple leaves in the spring undergo a transition from sink to source, and that sorbitol metabolism is tightly controlled and may be related to mechanisms that regulate sink activity.

4. Effects of fruits on rate of photosynthesis.

Several investigators have reported higher photosynthetic activity in leaves of fruiting than of nonfruiting apple trees. Salzer (1982) studied the photosynthetic activity of fully-developed leaves of four strains of 'Goldenspur Delicious'. The rate of photosynthesis in fruiting variants was nearly double that in non-fruiting clones. Fruits imported photosynthates from leaves 6 or more internodes away. Fujii and Kennedy (1985) observed that photosynthetic rates were elevated during bloom and again during rapid fruit growth (July to September). At both times CO₂ fixed per unit leaf area was greater in bearing than in non-bearing spurs; Antoszewski and Lenz (1982) reported similar effects. No effect of fruit was observed on photorespiration, leaf resistance, dark respiration, or transpiration (Fujii and Kennedy, 1985). Hansen (1971 a), however, observed higher transpiration in bearing than in defruited trees of 'Golden Delicious'. Stomatal aperture was greater in leaves of fruiting trees.

Rom and Ferree (1986 a) reported the presence of fruits did not affect rates of photosynthesis and transpiration in spur leaves. Photosynthesis and transpiration were highest at full bloom and shortly thereafter. No differences in carbohydrates and leaf number or area were observed between fruiting and non-fruiting spurs. The authors suggested that

photosynthesis and spur leaf area could limit early fruit development.

Sink-source relationships may explain the stimulating effects of fruits on the rate of photosynthesis. In fruiting apple trees, fruit are normally the dominant sinks (Hansen, 1967, 1970 b, 1982). Faust (1989) proposed that photosynthetic efficiency is determined by the presence of sinks and stated that, in general, sink strength is: fruit > shoot > root. The relationships between source and sink can explain carbohydrate assimilation and utilization in fruit trees (Hansen, 1982). Increasing the ratio of source size/sink size either by increasing the leaf area or reducing sink (fruit) numbers reduces the rate of leaf photosynthesis, while increasing fruit growth rate, and levels of certain components in both sources and sinks (Hansen, 1982). Hansen (1982) used different intensities of fruit thinning and kept leaf area per tree of heavily fruiting 'Golden Delicious' constant from July 9 to October. He observed that increasing leaf area/fruit reduced net assimilation rate (g dry matter increase per cm² leaf area), while increasing leaf starch content and specific leaf weight.

5. Evidence that carbohydrates play a role in fruit set of apple.

Faust (1989) lists three prerequisites for good fruit set in fruit trees: 1) formation of strong flower buds the previous season; 2) appropriate temperatures to assure good pollination and pollen tube growth; and 3) a high level of photosynthate for fertilized flowers and developing fruitlets. High flower density is associated with low fruit set as a percentage of total flowers (Heinicke, 1917). Howlett (1926) observed that at full bloom the petals contained from 67 to 95% of the free reducing sugars; the concentration increased very rapidly from tight cluster until full bloom, then dropped markedly. On the other hand, no significant increase in reducing sugars was observed in the receptacle between flower opening and petal fall. Higher activity of respiratory enzymes was observed in bearing branches than in non-bearing ones (Kazaryan et al., 1982). Khormenko (1978) observed that rates of both respiration and photosynthesis were highest during the first stage of fruit growth. Utilization of assimilates by a single reproductive organ was greatest during fruit growth and development, but utilization by the whole tree was greatest during flowering and fruit set. Therefore, apple trees with a heavy bloom lose larger amounts of carbohydrates because of loss of petals and higher respiration rates than do trees with light bloom. This

could account for the lower percentage of fruit set in trees with higher flower density.

Cultural practices may influence sink strength and consequently assimilate utilization. Examples of such practices are dwarfing rootstocks and ringing or scoring, which can increase sink strength of fruits by decreasing vegetative growth, thus favoring carbohydrate utilization by fruits. Good exposure of leaves to light can be achieved by judicious pruning and spacing, thus increasing source strength (Hansen, 1982).

Shading. Lakso (1984) reported that reducing light intensity 30% for 18 days after petal fall reduced initial set and final fruit size in potted 'Delicious' apple trees. Sorbitol injections overcame the effect of the shade, and stimulated set when injected into non-shaded trees. He suggested that carbohydrates are involved in fruit set. Lakso et al. (1984) reported that trunk injections of solutions containing 10% sorbitol from "pink" stage to 2 weeks after bloom increased fruit set in 6-year-old Starkrimson 'Delicious'/M.26 apple trees in the field. Final yield was increased by 20% with only a slight reduction in fruit size. The same treatment applied to potted trees of 'Delicious'/M.111 also markedly increased fruit set.

Byers et al. (1985) observed that shading of limbs of Starkrimson 'Delicious' for a 10-day period beginning 16 DAFB caused significant fruit abscission, whereas shading

for similar periods beginning 6, 26, or 36 DAFB did not. Terbacil, a photosynthetic inhibitor, applied to individual limbs at 400 ppm 6 or 16 DAFB significantly induced fruit drop, and applying 200 ppm to whole trees at 16 DAFB was even more effective. The authors concluded that the period from 16 to 26 DAFB represents a stage when fruits are especially susceptible to limitations in photosynthates. Subsequent experiments (Byers et al., 1990 b) demonstrated that shading (92%) of whole trees of Redchief 'Delicious' during 10 day periods beginning 10 to 25 DAFB caused significantly greater fruit abscission than did the same treatment beginning 5 or 30 DAFB or thereafter. Shading (92%) for 5 days, beginning 18 to 28 DAFB, caused significantly greater fruit abscission than shading beginning 11 or 33 DAFB. Spraying whole trees with terbacil (50 ppm) at 5, 10, or 15 DAFB significantly reduced fruit set. Shading reduced photosynthesis about 67%, while terbacil treatment reduced it more than 90% 72 hours after application, relative to control trees.

Polomski et al. (1988) reported that both terbacil and shade (92% for 10 days beginning 5 to 25 DAFB) reduced content of nonstructural carbohydrates in 'Delicious' fruitlets and caused fruit abscission. Shading materials were applied for 0, 5, or 10 days, then removed at 15, 20, 25, or 30 DAFB. At 15 and 20 DAFB, fruitlets shaded for 10 days had significantly lower carbohydrate content than did controls or fruitlets shaded for 5 days. Terbacil (50 and

100 ppm at 15 DAFB) markedly decreased photosynthesis and fruit dry weight, as well as content of total nonstructural carbohydrates, total sugars and reducing sugars. Terbacil at 100 ppm caused abscission of all fruitlets. In another experiment, both terbacil (75 ppm) and shade (92%) were tested in a factorial arrangement. The treatments were: 0 vs 10 days of shade, and terbacil at 0 or 75 ppm at 18, 23, or 28 DAFB. Fruit dry weight and levels of total sugars and reducing sugars were decreased by both shading and terbacil. Shading induced abscission of all fruits, and terbacil reduced fruit density approximately 70%.

Girdling or scoring. These treatments can increase fruit set of apple (Batjer, 1961; Batjer and Westwood, 1963; Burkhart and Westwood, 1964; Dennis and Edgerton, 1966; Hansen, 1981; Williams 1985). However, positive results are not always obtained (Batjer and Westwood, 1963; Greene and Lord, 1978; Rahemi, 1981). Response may depend upon timing, carbohydrate and nutrient (mainly nitrogen) status of the trees, or technique in girdling or scoring. Kraybill (1923) analyzed the first and second year wood from ringed 'McIntosh' apple trees. He found that ringing increased reducing sugars in branches about 30 days after treatment, but reduced moisture and nitrogen content. Mika and Antoszewski (1973) noted that bark ringing increased carbohydrate accumulation in apple shoots, while Hansen (1981) observed that ringing (2 mm wide ring of bark removed at bloom) or scoring (2 weeks after full bloom) 'Cox' and

'Golden Delicious' apple trees significantly increased fruit set and fruit dry matter.

Fruit thinning agents. Some studies suggest that fruit thinning compounds may act by interfering with photosynthate translocation from leaves to developing fruitlets. Schneider (1975) observed that naphthaleneacetic acid (NAA) reduced movement of ¹⁴C-sucrose from leaves to apple fruitlets. He concluded that NAA caused fruit thinning by establishing sinks in vegetative tissue, thereby reducing photosynthate transport to the growing fruitlets. In another study (Schneider, 1978 a), aqueous solutions of NAA, naphthalenacetamide (NAM), silver nitrate (AgNO₃), and galactose were used to observe the influence of thinning chemicals (NAA and NAM) on both carbohydrate transport and ethylene synthesis (induced by auxin; inhibited by AgNO₃; favored by galactose) or action. NAA application to entire limbs, or foliage only, reduced fruit set, but application to fruit only had no effect on fruit retention. AqNO3 had no effect on response to NAA, and galactose did not affect fruit retention. NAA decreased transport of ¹⁴C-sucrose from leaves to fruits. NAA (25 ppm), NAM (60 ppm) and ethephon (160 ppm) were applied to leaves of non-bearing trees of M.111, and 24 hours later the same leaves were treated with solutions containing either ¹⁴C-sorbitol or 14 C-sucrose. Of the 3 compounds tested, only NAM significantly reduced translocation of ¹⁴C from leaves to shoot tips. More ¹⁴C was found in shoot tips following

application of 14 C-sorbitol than of 14 C-sucrose, and lesser amounts of 14 C were translocated to the growing fruitlets (Schneider, 1978 a). The author concluded that the reduction of metabolite translocation from foliage to fruits is the primary mechanism responsible for NAA-induced fruit abscission, as previously hypothesized (Schneider, 1975). Application of auxin sprays (primarily NAA) to fruiting apple trees before "June" drop resulted in the following responses: 1) a decrease in the level of reducing sugars in the fruitlets; 2) a temporary stoppage or slowing of fruit growth; 3) unchanged capacity of the pedicel to translocate 14 C-IAA or 14 C-sucrose from leaves to fruitlets; 5) increased ethylene evolution 24 hours after NAA spray; and 6) increased water potential of the leaves.

Rootstocks. Several reports indicate that apple trees grafted on dwarf or semi-dwarf rootstocks have higher fruit set, or yield efficiency, or yield per unit land area. Hansen (1982) suggested that rootstock may influence assimilation and utilization of carbohydrates. In young trees a major effect of rootstock may be on relative sink strength, while in adult trees rootstocks may have a general effect on sink strength. Both Rao and Berry (1940) and Martin and Williams (1967) observed that dwarfed apple trees had higher levels of sugars and starch in the bark than standard trees.

Leaf area of 7- to 9-year-old trees of 'Reinette Champagne' on M.9 was about half that of trees on M.6

(Maidebura et al., 1978); however, when calculated on a per ha basis the total leaf surface of trees on M.9 was larger than that of trees on M.6, due to the closer spacing of trees on M.9. The authors also observed that the photosynthetic productivity of trees on dwarfing rootstock was higher than that of trees on semi-dwarfing or vigorous rootstocks.

Rud et al. (1978 a) observed that leaf chlorophyll content was higher in 'Jonathan' trees on M.9 than in trees on M.4. Leaf photosynthesis was also greater in trees of 'Jonathan' on M.9 than that of trees on M.4 (Rud et al., 1978 b).

Trunov and Muromtsev (1980) grafted scions of 'Melba', 'Korinchnoe Polosatae', 'Antonovka Obyknovennaya' and 'Onazhevoe' on either clonal stocks of Budagovski Paradise or on 'Kitaika' seedlings (<u>Malus prunifolia</u>). In a second experiment, 'Orazhevoe' was grafted on 'Kitaika' seedlings, or on clonal rootstock (PK-14, 49, 54-118, or 223). Photosynthetic productivity was highest in trees on the dwarfing Budagovski Paradise rootstock in the first experiment and in trees on the semi-vigorous rootstock No. 49 in the second experiment.

Dzieciol and Antoszewski (1984) studied ¹⁴C assimilate distribution in 'McIntosh' on M.7 rootstock using M.7, M.9, and A.2 as interstems; in a second experiment, 'McIntosh' was used on the following combinations of stocks: A.2/M.9/A.2; M.9/M.9/M.9; and M.9/A.2/M.9. ¹⁴C was

administered to all leaves. Distribution of radioactive assimilates 24 hours later was not significantly affected by interstem. Contents of soluble carbohydrates and phenolic compounds were significantly higher in the bark than in the wood, whereas starch was only slightly higher in the bark. Distribution of ¹⁴C assimilates was also studied in young 'Golden Delicious' apple trees on dwarfing and vigorous interstems (Dzieciol, 1985). 'Golden Delicious' scions were grafted in April on M.106 stocks with P.2 or A.2 interstems. The trees were held in a greenhouse and exposed to ¹⁴CO₂ for 1 hour on June 21, August 16, or September 20. Distribution of labelled assimilates was measured 48 hours after exposure to ¹⁴CO₂. Most of the labelled assimilates occurred in new growth in June, but in the roots in August and September. Interstem did not affect distribution.

Brown et al. (1985 a) measured carbohydrate content of Redchief 'Delicious' and 'Northern Spy' apple trees on both M.9 and M.111 rootstocks from March 1983 to April 1984. Dry weights of both above ground and below ground parts were higher in trees on M.111. Carbohydrate content followed a similar pattern. 'Northern Spy' had greater dry weight and carbohydrate content in the above ground parts than Redchief 'Delicious', whereas Redchief had greater dry weight and carbohydrate in underground parts. Above ground starch and below ground sorbitol and soluble sugars did not follow the same pattern.

Brown et al. (1985 b) recorded leaf expansion, carbon (C) exchange rate (CER), mass carbon transfer (MCT) and carbohydrate pools in one-year-old trees of Redchief 'Delicious' and 'Northern Spy' on M.9 and M.111 during an entire growing season. CER was higher in trees on M.111 than in those on M.9, and MCT was higher in 'Northern Spy' leaves than in Redchief 'Delicious' leaves. Trees on M.111 had significantly higher daily starch and sorbitol accumulation as percent of CER than trees on M.9. Redchief showed a net dry weight gain over a 24 hours period, but 'Northern Spy' did not. Starch concentration increased throughout the season in all trees. Rates of sorbitol and starch accumulation in the leaves was the highest at midseason and declined thereafter, while sucrose accumulation rate increased beginning at mid season.

C. <u>Summary</u>.

Considerable evidence exists in the literature that carbohydrates are important in apple fruit setting and retention. Therefore, my goal was to establish whether the effects of several treatments/cultural practices could be explained by their effects upon carbohydrate content of either flower cluster bases or bark.

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II. GENERAL PROCEDURES FOR CARBOHYDRATE ANALYSIS

Flower cluster bases and bark of one-year-old branches were used for both sugar and starch analysis in all the experiments. The procedures used for sampling, material preparation, extraction of sugars and starch, chromatographic analysis of sugars and spectrometric determination of starch were identical for all experiments. Methods specific to individual experiments are reported in separate sections.

A. <u>Plant material</u>

The apple trees used were 5 to 28 years of age, depending on experiment. Flower cluster bases consisted of only current season's tissue, while the bark tissue was taken from one-year-old branches (previous year's growth).

B. <u>Sampling procedure and sample preparation</u>

The flower cluster bases were sampled at random at a height of 1.5 to 2.5 m all around the canopy at full bloom. A minimum of 15 flower clusters were taken from each tree.

The bark tissue was removed with an 8 mm diameter cork borer. At every sampling date, 10 to 20 discs of bark were

taken at random from one-year-old branches of flowering limbs.

All samples were immediately placed in labelled plastic bags, which were sealed and kept on ice during transport to the laboratory. There, the leaves, flowers and pedicels were removed and discarded; the remaining tissues were placed in paper envelopes and dried at 70C in a circulating air oven. After drying, the envelopes were stored in a desiccator over anhydrous calcium sulfate. The tissues were then ground in a Wiley mill to pass a 40 mesh screen. The ground samples were kept in glass vials, sealed with cork stoppers, in a desiccator until they were extracted.

C. Extraction and analysis of soluble carbohydrates

1. Extraction.

One hundred mg of dry tissue was weighed and placed in a glass centrifuge tube. 3.5 ml of 80% ethanol (ETOH) was added to the tube, which was then agitated every 10 minutes for a total of 30 minutes. The tube was centrifuged at 455 g for 5 minutes and the supernatant transferred to a 100 ml round bottom flask. The pellet was resuspended in 3.5 ml 80% ETOH and the extraction repeated twice. The tube containing the pellet was covered with "Parafilm" and stored in a freezer at -18C until extracted for starch analysis.

The ethanol was evaporated to dryness at 40C in a rotary vacuum evaporator.

2. Preparation of standards.

A standard sugar solution was prepared by adding 0.25 g each of sorbitol, fructose, glucose and sucrose to one 50 ml volumetric flask. Inositol (0.1 g) was weighed into a small beaker and enough 50 ETOH was added to dissolve it. The inositol solution was then added to the 50 ml flask. The small beaker was washed with 80% ETOH, the washing added to the flask, and the total volume was adjusted to 50 ml with 80% ETOH. This sugar standard solution was held at 5C for up to one month.

Standard sugar solution (500 μ l) was added to one dram vials and the 80% ETOH evaporated in a gentle stream of nitrogen. When completely dry, the vials were stored in a desiccator.

3. Conversion of sugars to oximes.

The derivatization solution consisted of: 1.5 g of hydroxylamine-mono-hydrochloride and 0.125 g of B-phenyl-Dglucopyranoside (internal standard) in 50 ml of pyridine (silylation grade). The sugars were then transformed to oximes (Holligan, 1971; Roper et al., 1988). In an exhaust hood, 1.5 ml of the derivatization solution was added to each of the round bottom flasks containing dry residues of the extracts. The flasks were covered with "Parafilm" and shaken every 5 minutes for a period of 40 minutes. At this time all the sample extract that adhered to the internal wall had been dissolved.

A 1 ml aliquot from each flask was transferred to a one dram vial, and 1 ml of derivatization solution was added to each of 2 vials containing standard sugars. All vials were immediately closed with Teflon^R-lined serum cap. For each set of samples to be analyzed 2 vials containing the standard sugars were used. Vials containing either sample extract or standard sugars were gently agitated in a vortex, then placed in a sand bath at 75C in an exhaust hood. The vials were agitated gently in a vortex after 20 and 40 minutes. After 60 minutes at 75C, the vials were allowed to cool to room temperature (about 10 minutes). Hexamethyldisilazane (HMDS, 1 ml) followed by trifluoroacetic acid (TFA, 0.1 ml) were then added to each vial. The oximes of sugars were converted to trimethylsilyl ethers by HMDS (Holligan, 1971; Sweeley et al., 1982), while the TFA was used to avoid problems in the GC determination if any water was present (see Holligan, 1971).

4. Gas chromatography.

The instrument used for chromatography was a Varian 3700 gas chromatograph with a glass column (2.0 m * 2.0 mm ID), packed with 3% OV-17 on Chromosorb WHP 80/100. Temperatures were: injector, 260C; flame ionization detector, 330C; and oven maximum temperature, 350C. The oven temperature was programmed to remain at 150C for 2 minutes following injection, then rise to 282C at 5C/min. Total run time was 38 min. The gas pressures were: air, 4.2 kg/cm²; hydrogen, 2.8 kg/cm²; and nitrogen (carrier gas), 4.2 kg/cm². The flow rate was 29 ml.min⁻¹.

A Spectra Physics SP 4100 integrator was used to quantify response. This was calibrated using standard sugars to permit automatic calculation of the amounts of sugars present in the samples. Two aliquots of the derivatized standard sugars (1 μ 1) were injected for calibration before starting sample injection. A new calibration was performed after 20 samples had been injected.

D. Analysis of starch.

1. Enzymatic hydrolysis.

The insoluble residues from 100 mg samples of either flower cluster bases or bark were used for quantitative

determination of starch. Potato starch was used as a standard, 10 mg being added to a tube containing 1 ml of distilled water: 1 ml of distilled water was used as a blank. Acetate buffer (1.5 ml of a 0.1 M solution, pH 5) was added to each sample. All tubes were gently agitated in a vortex and left for 60 minutes at 100C in a sand bath. After the tubes had cooled to room temperature, 100 μ l of a freshly prepared solution (0.166 g/ml in acetate buffer) of amyloglucosidase (Boehringer Mannheim, approximately 6 units/mg) was added to each of 3 replicate samples of extract, starch, or blank. The tubes were gently agitated in a vortex and placed in a 55C water bath for 16 hours. The blank and starch standards were transferred to 50 ml volumetric flasks, and brought to volume with distilled water, whereas the sample tubes were brought to 15 ml final volume.

2. <u>Preparation of standards</u>.

A standard solution of β -D-glucose (Sigma) at 1 mg/ml (5.56 μ mole/L) in 0.1% benzoic acid was prepared to construct a standard curve for starch. The β -D-glucose standard was diluted with 4 parts of distilled water prior to use and 100 μ l were transferred to test tubes. Water (250 μ l) was used as a blank. Three replicates were used per concentration.

3. <u>Quantification of glucose</u>.

Glucose was converted to gluconic acid with glucose oxidase, releasing peroxide. The peroxide then reacted with O-dianisidine in the presence of peroxidase to give the oxidized form of O-dianisidine (brown). A 2.5 ml volume of color reagent (1.65 ml of 0.25% aqueous O-dianisidine dihydrochloride, Sigma 510-50, plus 500 units of glucose oxidase from <u>Aspergillus niger</u> and 100 units of purpurogallin from <u>Armoracia lapathifolia</u> in 100 ml aqueous buffer) was added to each sample. The solutions were left for 40 minutes at room temperature (20C), then the absorbance at 440 nm was read in a Shimadzu UV-260 spectrophotometer. Absorbance was plotted against the concentration of glucose in the standards; a regression through the origin gave the following equation:

 μ g glucose (Y) = a + bx, where x = absorbance at 440 nm, and a = 0.

All the glucose standard curves gave equations with a coefficient of correlation (r) > 0.99.

The amount of starch per 100 mg sample was calculated according to the following formula:

mg starch = μ g glucose^X * final vol^Y/ml aliquot^Z * 0.9/1.0

 $x = \mu g$ glucose obtained from the equation generated by the glucose standard curve (μg glucose = absorbance * slope)

y = final volume of sample extract

z = volume of sample extract used

Substituting the actual volumes used, one obtains:

mg starch = μ g glucose * 15 ml/0.25 ml * 0.9 * 0.001

= μg glucose * 0.054

For each set of samples analyzed, the starch standard was used to calculate recovery.

E. <u>Statistical analysis of the data</u>

Data for initial and final fruit set in percentage, transformed to $\arcsin \sqrt{3}$, and for each carbohydrate analyzed, were subjected to analysis of variance (ANOVA), using values for each replicate tree. Duncan's multiple range test (DMRT) was used to separate means wherever F values were significant. Correlation coefficients (r) were determined for final set vs. levels of each carbohydrate analyzed, using all individual values within an experiment without factoring out treatments (rootstock, shading, strain, etc).

F. Literature Cited

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III. FRUIT SET VS. CARBOHYDRATE CONTENT IN BARK AND CLUSTER BASES: EFFECTS OF SHADING, SCORING, OR GIRDLING.

Shading after full bloom reduces fruit set of apple (Berüter, 1985 b; Byers et al., 1990 a, b; Doud and Ferree, 1980; Lehman et al., 1987; Polomsky et al., 1988; Rom and Ferree, 1984; Schneider, 1978 a). Shading (8% full sun) 'Stayman' apple trees for periods of 5 to 10 days beginning after petal fall reduced set, and decreased the content of reducing and non-reducing sugars and starch of the fruitlets (Polomski et al., 1988). Sorbitol injection (Lakso, 1984), as well as girdling or scoring, increases set of apple (Batjer, 1961; Batjer and Westwood, 1963; Buszard, 1983; Dennis and Edgerton, 1966; Griggs and Schrader, 1940; Marro and Deveronico, 1981; Priestley, 1976; Schneider, 1978 a). If carbohydrate levels are responsible for the effects of these various treatments on fruit set, shading should reduce, whereas girdling should increase, carbohydrate content. My purpose was to test the effects of both shading and girdling on fruit set and carbohydrate content.

Materials and Methods

<u>Experiment 1</u>. <u>Redchief 'Delicious'/M.7</u>. The effects of shading and scoring on apple fruit set vs. carbohydrate content were evaluated at the Clarksville Research Station,

Clarksville, Michigan. The following treatments were tested on Redchief 'Delicious' on M.7 EMLA, planted in 1980, using a randomized complete block design with four replications, one tree per plot:

- a) non-treated control
- b) 60% shade in the fall (from September 15 to November 15 of 1984)
- c) 30% shade in the spring 1985 (from green tip to the end of "June" drop)*
- d) 60% shade in the spring 1985 (from green tip to the end of "June" drop)*
- e) scoring of the trunk at full bloom

A framework of galvanized iron pipe was built over the trees used for treatments b, c, and d. Shade cloth (Lumite Fabric by Chicopee, Cornelia, GA, USA) was fastened to this framework so as to cover the entire canopy. No direct sunlight could reach the leaves without passing through the cloth. The frame was not covered at the base (60 cm from the soil). Temperatures at the middle height of the canopy of control and 60% shade trees were recorded during the fall of 1984. Maximum, minimum, and current temperatures are shown in Table A.

^{*} The shade cloth was removed during bloom to permit insect pollination

The scoring treatment consisted of a single cut with a sharp knife through the bark, encircling the main trunk 20 cm above the graft union.

On each tree 50 flower clusters were tagged on twoyear-old spurs distributed at random around the tree canopy. The average number of flowers per cluster was calculated from counts made on 50 randomly selected flower clusters on four experimental trees. Fruits were counted at 25 DAFB and again after "June" drop, and initial and final fruit set were calculated.

Cluster bases (20 per tree) were sampled at full bloom, and 8 mm diameter bark discs (15 per tree at each sampling) were collected from one-year-old terminal branches of flowering limbs, both at full bloom and 15 days after full bloom.

Experiment 2. 'Empire' and 'MacSpur'. In 1986, a second experiment was performed at the Horticultural Teaching and Research Center (MSU), East Lansing, Michigan. A randomized complete block design with two replicates per block was used. Because the cultivars ('Empire'/M7 and 'MacSpur'/M7) were not randomized, they were treated as blocks in statistical analysis.

Treatments:

- a) control (full sunlight)
- b) 30% shade from green tip to pink bud, plus 85% shade from petal fall to leaf fall*

- c) 60% shade from green tip to leaf fall*
- d) girdling of the main trunk by removal of a bark strip 2 mm wide, encircling the trunk at 20 cm above the graft union, the wound being covered with grafting compound

On each tree 100 flower clusters on two-year-old spurs were tagged. Fruits were counted at 25 DAFB and again after "June" drop, and the data were used to calculate initial and final fruit set.

Cluster bases were collected at full bloom, whereas bark samples were taken at full bloom and 7, 25, and 65 days (1 month after "June" drop) after full bloom. The procedures of sampling, material preparation, carbohydrate extraction and quantification, and statistical analysis were the same as described above for experiment 1.

Photon flux density (PFD) at different sites of the canopy was measured at two dates in September of 1986, using a Quantum LI 188 radiometer with a sensor Q 5227 S (Table B). Much rain fell in September and solar radiation was limited. The data in Table B were recorded when the sky was overcast, and therefore the values are low.

The shade cloth was removed from pink bud stage until petal fall to allow insect pollination. The same kind of framework and tree covering with shade cloth was used as described above for experiment 1.

^{*} The shade cloth was removed from pink bud stage until petal fall to permit insect pollination

				Observations at time of		
)ate	Time	Shade (%)	Max	Min	Current	temperature reading
October, 1	9:30 am	0	17.8	0.6	8.3	clear
		60	15.6	0.0	8.3	
October, 2	11:15 am	0	20.6	2.8	15.0	clear
		60	16.1	2.2	13.9	
October, 3	12:30 pm	0	17.8	10.6	17.2	clear
		60	17.8	10.0	16.7	
October, 6	5:15 pm	0	20.0	1.1	18.9	overcast
		60	20.6	0.6	19.4	
October, 10	9:00 am	0	13.3	2.2	11.1	overcast
		60	13.3	2.2	10.0	
October, 16	3:00 pm	0	21.1	7.2	20.6	clear
		60	20.6	6.7	20.6	
lovember, 15	3:30 pm	0	16.1	-8.3	-8.3	cloudy, some
		60	21.1	-8.9	-8.9	rain

Table A. Temperature conditions at the middle part of tree canopy of control and 60% shade trees. Clarksville Horticultural Experiment Station. Clarksville, MI. 1984.

Table. B. Photon flux density (PFD) in μ mol m⁻²sec⁻¹ in 'Empire' and 'NacSpur' at two dates. Horticultural Teaching and Research Center, E. Lansing, MI. 1986.

			S	ites of measur	ement in the	canopy		
Shade	Under canopy	Middle-1.6m from ground	C:	anopy border -	1.6m from g	round	Tree Top ^z	
(%)	(20cm)		North	South	E as t 	West		
			9-9-8	5 (3:30 to 4:0	0 pm)			
0	62±27	151±98	313±111	300±69	266±152	338±152	441±62	
60	26±5	20±17	56±25	78±53	61±26	64±26	120±79	
85	20±3	16±14	32±11	35±4	36±19	34±13	38±21	
			24-9	7-86 (4:20 to)	5:40 pm)			
0	97±31	33±7	233±90	353±86	221±87	359±94	542±170	
60	26±3	20±10	56±21	146±92	57±19	134±56	146±47	
85	25±12	10±5	27±12	59±37	24±6	45±21	46±10	

 2 In the shaded trees, PFD was measured at 20 cm under the shading fabric, while in control trees the PFD was measured at 20 cm above the tree top.

Results

Experiment 1. Redchief 'Delicious'/M.7. Although shading in the spring appeared to reduce set, analysis of variance (ANOVA) of the transformed percentage (arcsin $\sqrt{*}$) of initial and final set indicated no significant effect of treatment (Table 1). Final fruit set was significantly correlated with initial fruit set (Table 1, Figure 1). Sorbitol was the major sugar in the cluster base at full bloom. Effects of the treatments on levels of carbohydrates in the cluster base tissue at full bloom were nonsignificant by F test, p < 0.05 (Table 1). Similarly, correlation coefficients between either initial or final set and each sugar, total water soluble sugars, or starch, were non-significant.

Similar results were obtained when ANOVA ($F_{\alpha} = 0.05$) was used to compare the effect of the treatments on the levels of carbohydrates of the bark tissue at either full bloom (Table 2) or 15 days thereafter (Table 1). Sorbitol was again the major sugar in the bark tissue at both dates. Neither initial nor final set was significantly correlated with levels of carbohydrates in the bark at full bloom (Table 2) or 15 days thereafter (Table 3).

The sorbitol content of the cluster base tissue was higher ($t_{\alpha} = 0.01$) than that of bark, both at full bloom and 15 days after full bloom. On the other hand, bark tissue had higher levels of fructose ($t_{\alpha} = 0.01$) and glucose ($t_{\alpha} =$

0.05) than cluster bases, at full bloom. The levels of sorbitol, fructose, and glucose in the bark decreased from full bloom to 15 days later ($t_{\alpha} = 0.05$), whereas no such decrease occurred with sucrose and starch.

Experiment 2. 'Empire' and 'MacSpur'. Both shading and girdling decreased initial and final set (Table 4). The 85% shade treatment was more effective in reducing set. Although 60% shade had similar effects upon initial set, final set was much lower under 85% shade. "June" drop was negligible in both control and girdled trees.

None of the treatments significantly affected sugar or starch levels of the cluster base tissue (Table 4). Sorbitol was again the main sugar while very low levels (0.08% to 0.10%) of inositol were detected. Final set was correlated with initial set (Table 4, Figure 2), but no significant relationship was found between either initial or final set and each sugar or starch concentration (Table 4). Neither shade nor girdling affected the levels of sugars and starch in the bark at full bloom (Table 5). Correlation coefficients between final set and levels of sugars and starch were non-significant (Table 5).

Although the treatments did not affect sorbitol, fructose, inositol, sucrose, water soluble sugars and starch content of the bark at 7 days after full bloom, glucose level was increased by girdling (Table 6). Both initial and

final set were significantly correlated with sucrose content, but not with any of the other compounds.

Differences among treatments were much more pronounced at 25 DAFB (Table 7). Heavy shading (85%) decreased bark sorbitol, fructose, glucose and inositol, but did not significantly affect the levels of sucrose and starch. Although 60% shade appeared to reduce the levels of all compounds, only sorbitol levels were reduced significantly. Both shading treatments decreased total water soluble sugar level, whereas girdling did not affect them. Girdling of the main trunk significantly increased the levels of glucose and starch, but effects on the levels of other sugars were non-significant. Levels of all compounds except sucrose were significantly higher in girdled trees than in those that were heavily shaded, and levels of fructose, glucose, inositol, and starch were higher than in trees with 60% shade. Final fruit set was not positively correlated with content of any carbohydrate (Table 7).

Carbohydrate levels in the bark at 60 DAFB were also affected by treatment (Table 8). Contents of sorbitol, fructose, glucose, water soluble sugars and starch were lowest in heavily shaded (85%) and intermediate in 60% shade trees. Inositol content was not affected by any of the treatments. Sucrose levels were decreased by 85%, but not by 60% shade. Final fruit set was positively correlated with levels of all compounds except inositol (Table 8, Figures 5, 6, 7, 8, 9, and 10).

Girdling decreased leaf size on both terminal shoots and spurs (Table 9). Neither shade treatment significantly affected the area of spur leaves, but 60% shade increased the size of leaves on terminal shoots. Girdling increased specific dry weight (LSDW) of spur, but not of shoot leaves, whereas both shading treatments reduced LSDW. Correlation coefficients (Table 9, Figures 11 and 12) indicate that final fruit set was positively correlated with both spur and shoot LSDW, but not with area per leaf (Table 9).

The leaves of shaded trees were lighter green in color, and horizontal or curled downward; in the fall, leaves became yellow sooner and developed more red color than those of control trees. The lighter green color of leaves of shaded trees was unexpected because shading usually increases leaf chlorophyll content (Devlin and Witham, 1983; Leopold and Kriedemann, 1975). However, the shaded trees may have been deficient in nitrogen, since they were shaded during the entire growing season except for 1 week during bloom. Roots require carbohydrates for N uptake and metabolism (Devlin and Witham, 1983; Faust, 1989). Sams (1980) applied shade (91%) to one-year-old potted cherry trees from the 11 to 15 leaf stage until the end of the growing season, but observed no increase in chlorophyll per unit leaf area. However, shade increased leaf chlorophyll per unit dry weight and per unit volume. Girdled trees had some leaf yellowing throughout the growing season, and some

leaves had reddish margins; the leaves were curled up in a narrower "V" shape than leaves of control trees.

Shaded trees had thinner and longer spurs and terminal branches at the end of the growing season compared to control trees. Although girdled trees had shorter terminals, no differences in spur thickness and length was evident.

A scale of 1 to 5 was used for intensity of fruit color. Fruits on shaded trees were greener (grade 1 and 1.5 for 85% and 60% shade, respectively) than control or girdled trees, which both graded 4.5. Mean fruit weights (g) at harvest were: 158, 136, 130, and 122 g for control, 60% shade, 85% shade, and girdled trees, respectively (SD = 10.28). The fruitlets on shaded trees were already smaller than those on control trees at 25 DAFB, while fruitlets on girdled trees at that time were similar to control fruitlets.

Treatment	Fruit Se	t (%)		Cart	ohydrate	(% dry wei	ght)		
	Initial	Final	Sorbitol	Water Fructose	Soluble (Glucose	Carbohydra Inositol	ites Sucrose	Total	Starch
Control	26.7ab ^x	20.3a	6.90	0.41	0.33	0.19	0.82	8.65	0.67
60% shade in the fall of 1984 (Sept. 15 - Nov 15	27.5ab	20.9a	6.47	0.37	0.33	0.18	0.71	8.06	0.58
60% shade from BB to PB and from PF to FS ^Y	16.9Ь	14.1b	6.12	0.33	0.30	0.16	0.81	7.72	0.62
30% shade from BB to PB and from PF to FS	25.5 a b	19.9 a	7.36	0.37	0.28	0.16	0.67	8.84	0.49
Scoring of the trunk at FB ^Y	36.8a	20.8a	6.85	0.41	0.33	0.17	0.82	8.58	0.62
r ^z (initial set vs carbohydrate conte	nt)		0.283ns	0.404ns	0.187ns	0.346ns	0.185ns	0.349ns	-0.06ns
r (final set vs init set or carbohydrat content)	0.579 [*] fal e	*	0.063ns	0.098ns	-0.169ns	0.009ns	-0.254ns	-0.011ns	-0.184r

Table 1. Effects of shading and scoring on fruit set and carbohydrate levels in the flower cluster base of

^X Mean separation within columns by DMRT, p < 0.1.

Y BB = Bud Break; PB = pink bud; FS = Fruit Set (after 'June drop' ended); FB = Full Bloom; PF = Petal Fall. ² r value required for significance with 18 df = 0.444 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .



Figure 1. Correlation between final and initial set (% of flowers) in Redchief 'Delicious'. Clarksville, MI. 1985.

Treatment	Carbohydrate (% dry weight) [%]									
	Sorbitol	Water Fructose	Soluble Glucose	Carbohydra Inositol	tes Sucrose	Total	Starch			
Control	3.97	1.06	1.31	0.06	0.35	6.75	0.50			
60% shade in the fall of 1984 (Sept 15 - Nov 15)	3.81	0.94	1.17	0.08	0.32	6.31	0.32			
60% shade from BB to PB and from PF to FS ^y	3.77	1.03	1.30	0.07	0.40	6.57	0.36			
30% shade from B8 to PB and from PF to FS	3.76	1.06	1.27	0.04	0.73	6.86	0.49			
Scoring of the trunk at FB ^y	3.70	1.01	1.20	0.07	0.40	6.38	0.55			
r ^z (initial set vs carbohydrate content)	0.022ns	0.016ns	-0.124ns	-0.049ns	-0.101ns	-0.091ns	0.248ns			
r (final set vs initial set or carbohydrate content)	0.083ns l	-0.180ns	-0.241ns	-0.266ns	-0.038ns	-0.095ns	0.323ns			

Table 2. Effects of shading and scoring on carbohydrate levels in the bark of one-year-old branches of 'Redchief' apple trees at full bloom in 1984 - 1985. Clarksville, MI.

^X There was no significant difference between levels of carbohydrate within same column.

Y BB = Bud Break; FS = Fruit Set (after 'June drop' ended); FB = Full Bloom; PB = Pink Bud.

² r value required for significance with 18 df = 0.444 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .

.

Treatment	Carbohydrate (% dry weight)									
	Sorbitol	Water Fructose	Soluble (Glucose	Carbohydra Inositol	tes Sucrose	Total	Starch			
Control	3.16e ^x	0.74a	1.10a	0.06	0.15	5.21	0.54			
60% shade in the fall of 1984 (Sept 15 - Nov 15)	2.82ab	0.68 e b	1.00 a b	0.07	0.04	4.61	0.33			
60% shade from BB to PB and from PF to FS ^Y	2.086	0.496	0.74b	0.10	0.20	3.61	0.47			
30% shade from BB to PB and from PF to FS	3.12 a	0.74 a	1.12a	0.11	0.13	5.22	0.38			
Scoring of the trunk at FB	3.55a	0.86a	1.31a	0.06	0.14	5.92	0.46			
r ^Z (initial set vs carbohydrate content;	0.271ns	0.238ns	0.231ns	-0.182ns	0.173ns	0.257ns	0.192ns			
r (final set vs initia set or carbohydrate content)	0.086ns l	0.071ns	0.075ns	-0.345ns	0.205ns	0.093ns	0.004ns			

 Table 3. Effects of shading and scoring on carbohydrate levels in the bark of one-year-old branches of

 'Redchief' apple trees at 15 days after full bloom in 1984 - 1985. Clarksville, MI.

^X Nean separation by DMRT, p < 0.1.

Y BB = Bud Break; FS = Fruit Set (after 'June drop' ended); FB = Full Bloom; PB = Pink Bud.

² r value required for significance with 18 df = 0.444 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .

		Carbohydrate (% dry weight)										
	Fruit s	et (%)		Water	Soluble Ca	8		Starch				
	Initial	Final	Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total				
() <u>Cultivar</u>												
'Empire'	6.20	4.43	4.19	0.22	0.13	0.08	0.50	5.12	0.43			
'MacSpur'	12.00	8.88	3.27	0.20	0.14	0.09	1.07	4.77	0.35			
3) <u>Treatment</u>												
1- Control	16.35a ^x	15.35a	4.18	0.19	0.11	0.08	0.75	5.31	0.41			
2- 30% shade from GT to B and IS% shade from PF to LF ^y	2.90c	0.11d	3.58	0.21	0.13	0.09	0.55	4.56	0.40			
3-60% shade from GT to B and from PF to LF	7.35b	1.40c	3.57	0.20	0.15	0.10	0.94	4.96	0.39			
4-Girdling of the trunk at GT	9.75b	9.75b	3.59	0.26	0.14	0.08	0.90	4.97	0.34			
.z (initial set vs perbohydrate cont	ent)		-0.067ns	-0.079ns	-0.055ns	-0.104ns	0.333ns	0.079ns	-0.177			
final set vs ini set or carbohydra	0.903* tial te	•	0.166ns	0.037ns	-0.171ns	-0.248ns	0.171ns	0.283ns	-0.094			

Table 4. Effects of shading and girdling on fruit set and carbohydrate levels in cluster bases of 'Empire' and /MacSnur/ annie trees. Horticultural Teaching and Research Center E Lansing MI (1986)

Y GT = green tip, B = bloom, PF = petal fall, LF = leaf fall.

² r value required for significance with 14 df = 0.497 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .

** = Significant at p < 0.01; ns = non significant at p < 0.05.



Figure 2. Correlation between final and initial set (% of flowers) of 'Empire' and 'MacSpur'. East Lansing, MI. 1986.

(
			Carbohyd	rate (% dry	/weight) ^X		
		Water	Soluble Ca	rbohydrate	3		Starch
	Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total	
A) <u>Cultivar</u>							
'Empire'	2.31	0.38	0.31	0.03	1.12	4.15	0.20
'NacSpur'	2.62	0.27	0.19	0.02	2.00	5.10	0.27
B) <u>Treatment</u>							
1- Control	2.53	0.32	0.25	0.02	1.55	4.67	0.22
2- 30% shade from GT to B and 85% shade from PF to LFY	2.45	0.33	0.27	0.02	1.47	4.54	0.23
3-60% shade from GT to B and from PF to LF	2.73	0.37	0.27	0.04	1.55	4.96	0.25
4-Girdling of the trunk at GT	2.14	0.28	0.22	0.03	1.67	4.34	0.25
r ^Z (initial set vs carbohydrate content)	0.199ns	-0.264ns	-0.360ns	-0.283ns	0.493ns	0.246ns	0.209ns
r (final set vs initial set or carbohydrate content	-0.111ns	-0.274ns	-0.309ns	-0.139ns	0.337ns	0.005ns	0.053ns
^X Mean separation within c ^Y GT = green tip, B = bloo ^Z r value required for sig fruit set were transformed ns = non significant at p	columns by DH m, PF = peta nificance wi I to arcsin V < 0.05.	RT, p < 0.0 l fall, LF = th 14 df = 1 %.	5. = leaf fall 0.497 (p <	0.05). Da	ta in perce	ntage of init	ial and final

Table 5. Effects of shading and girdling on carbohydrate levels in bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, at full bloom. Horticultural Teaching and Research Center, E. Lansing, MI (1986).

			Carbohyd	rate (% dry	/weight)				
	Water Soluble Carbohydrates								
	Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total			
A) <u>Cultivar</u>									
'Empire'	2.69	0.35	0.38	0.04	1.00	4.46	0.26		
'MacSpur'	1.70	0.28	0.22	0.04	1.13	3.37	0.27		
) <u>Treatment</u>									
1- Control	2.46	0.35	0.306 ^x	0.04	1.29	4.44	0.25		
2-30% shade from GT to B and 15% shade from 1F to LF ^Y	2.05	0.30	0.27b	0.03	0.80	3.46	0.23		
3-60% shade rom GT to B and nd from PF to LF	1.90	0.26	0.22Ь	0.03	0.99	3.40	0.26		
4-Girdling of he trunk at GT	2.40	0.34	0.41a	0.04	1.18	4.37	0.30		
z initial set vs arbohydrate content)	-0.085ns	0.063ns	-0.127ns	0.334ns	0.654**	0.019ns	0.143		
final set vs initial et or carbohydrate content	0.117ns	0.194ns	0.104ns	0.394ns	0.640**	0.156ns	0.219		

Table 6. Effects of shading and girdling on carbohydrate levels in bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, at 7 days after full bloom. Horticultural Teaching and Research Center, E. Lansing, MI (1986).

** = Significant at p < 0.01; ns = non significant at p < 0.05.


Figure 3. Correlation between initial fruit set (% of flowers) and levels of sucrose in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 7 DAFB. East Lansing, MI. 1986.



Figure 4. Correlation between final fruit set (% of flowers) and levels of sucrose in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 7 DAFB. East Lansing, MI. 1986.

			Carbohyd	rate (% dry	/weight)		
		Water Soluble Carbohydrates					
	Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total	
N) <u>Cultiver</u>							
'Empire'	2.88	0.53	0.58	0.06	0.20	4.25	0.84
'NacSpur'	2.19	0.51	0.46	0.05	0.38	3.59	0.47
3) <u>Treatment</u>							
1- Control	3.33a ^x	0.63ab	0.60b	0.06ab	0.46	5.08a	0.61b
2- 30% shade from GT to B and 15% shade from PF to LFY	1.64c	0.22c	0.19c	0.04c	0.20	2.29Ь	0.30ь
3-60% shade from GT to B and from PF to LF	2.21bc	0.33bc	0.33bc	0.05bc	0.24	3.16b	0.336
4-Girdling of the trunk at GT	2.97ab	0.89a	0.97 a	0.07a	0.26	5.16 a	1.38a
.Z (initial set vs :arbohydrate content)	0.447ns	0.476ns	0.367ns	0.059ns	0.367ns	0.496ns	0.152r
(final set va initial set or carbohydrate	0.117ns	0.194ns	0.104ns	0.394ns	0 .368ns	0.156ns	0.219r

Table 7. Effects of shading and girdling on carbohydrate levels in bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, at 25 days after full bloom. Horticultural Teaching and Research Center, E. Lansing, MI (1986).

Table 8. Effects of	shading and girdling on	carbohydrate	levels in bari	k of <mark>one-yea</mark> r-o	ld branches of	'Empire'
and 'MacSpur' apple	trees, at 60 days after	full bloom.	Horticultural	Teaching and R	esearch Center,	E.
Lansing, MI (1986).						

		Carbohydrate (% dry weight)						
	Sorbitol	Water Fructose	Soluble Ca Glucose	rbohydrate: Inositol	s Sucrose	Total	Starch	
A) <u>Cultivar</u>		*****		•••••				
'Empire'	4.15	0.38	0.42	0.05	0.97	5.97	2.73	
'MacSpur'	3.78	0.55	0.50	0.04	1.35	6.22	1.83	
B) <u>Treatment</u>								
1- Control	4.80a ^X	0.586	0.58b	0.05	1.42 a b	7.43a	2.925	
2- 30% shade from GT to B and 85% shade from PF to LF ^Y	2.45c	0.21d	0.21d	0.04	0.58c	3.49c	0.55d	
3-60% shade from GT to B and and from PF to LF	3.49b	0.35c	0.33c	0.05	0.96bc	5.18b	1.32c	
4-Girdling of the trunk at GT	5.09a	0.71a	0.73a	0.05	1.67a	8.25a	4.32a	
r ^z (final set vs initial set or carbohydrate content	0.795**	0.841**	0.833**	0.279ns	0.820**	0.842**	0.644*'	

Y GT = green tip, B = bloom, PF = petal fall, LF = leaf fall.

² r value required for significance with 14 df = 0.497 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} . ** = Significant at p < 0.01; ns = non significant at p < 0.05.



Figure 5. Correlation between final fruit set (% of flowers) and levels of sorbitol in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 60 DAFB. East Lansing, MI. 1986.



Figure 6. Correlation between final fruit set (% of flowers) and levels of fructose in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 60 DAFB. East Lansing, MI. 1986.



Figure 7. Correlation between final fruit set (% of flowers) and levels of glucose in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 60 DAFB. East Lansing, MI. 1986.



Figure 8. Correlation between final fruit set (% of flowers) and levels of sucrose in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 60 DAFB. East Lansing, MI. 1986.



Figure 9. Correlation between final fruit set (% of flowers) and levels of total water soluble carbohydrates in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 60 DAFB. East Lansing, MI. 1986.



Figure 10. Correlation between final fruit set (% of flowers) and levels of starch in the bark of one-year-old branches of 'Empire' and 'MacSpur' apple trees, 60 DAFB. East Lansing, MI. 1986.

		Area per (cm ²)	r leaf	LSDW (mg/cm ²) at the end of the growth season		
		Spur Te	erminal	Spur	Terminal	
A)	<u>Cultivar</u>					
	'Empire'	18.58	34.15	7.70	8.83	
	'MacSpur'	19.78	38.38	8.14	9.85	
B)	<u>Treatment</u>					
-	Control	21.53a ^X	36.78b	9.20b	12.33a	
irc Ind Irc	30% shade om GT to PB 1 85% shade om PF to LF ^Y	17.73ab	36 . 56b	6.00c	5.63b	
). ST frc	60% shade to PB and om PF to LF	20.5ab	42.98a	6.60c	6.18b	
4.0 the at	Girdling of ≥ main trunk GT	16.95b	28.78c	9.88a	13.23a	
r ^z (fj col	nal set vs umn)	0.312ns	-0.231ns	0.916*	* 0.843**	
x M y G z r 0.0 tra	ean separation T = green tip Value requir 5). Data in Nsformed to a	n within colu , B = bloom, ed for signi percentage o rcsin $\sqrt{3}$.	umns by D PF = pet ficance w f initial : ns = no	MRT, $p < 0.05$ al fall, LF = ith 14 df = 0 and final from n significant	leaf fall. .497 (p < uit set were at p < 0.05.	

Table 9. Effects of shading and girdling on fruit set, leaf size and leaf specific dry weight (LSDW) of 'Empire' and 'MacSpur' apple trees. Horticultural Teaching and Research Center, E. Lansing, MI. 1986.



Figure 11. Correlation between final fruit set (% of flowers) and spur leaf specific dry weight (LSDW) of 'Empire' and 'MacSpur' apple trees, at the end of the growing season (leaves starting to fall). East Lansing, MI. 1986.



Figure 12. Correlation between final fruit set (% of flowers) and leaf specific dry weight (LSDW) on terminal shoots of 'Empire' and 'MacSpur' apple trees, at the end of the growing season (leaves starting to fall). East Lansing, MI. 1986.

Discussion

Experiment 1. Redchief 'Delicious'/M.7. Shade (30 or 60%) during the fall of 1984 (from September 15 to November 15) affected neither fruit set nor carbohydrate content of cluster bases or bark of one-year-old branches of Redchief 'Delicious' in the spring of 1985 (Tables 1 - 3). The degree of shading may have been insufficient, as only 30-40% of full sunlight is probably sufficient for apple tree growth and development (Cain, 1972; Faust, 1989). Photosynthetic activity is low during fall because carbohydrates have accumulated in the leaves (Hansen, 1970 b), and because mature leaves usually have low photosynthetic activity (Daie, 1985). During the spring, however, photosynthetic activity is normally high in expanding young leaves, especially during flowering and fruit development (Daie, 1985; Faust, 1989). Therefore shading should have had more effect in the spring than in the fall. However, the same shading treatments in the spring (30 and 60% shade = 70 and 40% full sunlight) also failed to affect either fruit set or carbohydrate levels significantly (p < 0.05). The effect of 60% shade on initial and final set (Tables 1 - 3), and on sorbitol, fructose and glucose levels in the bark at 15 DAFB was significant at the $\alpha = 0.1$, but not at $\alpha = 0.05$.

Scoring the trunk of Redchief 'Delicious' at full bloom affected neither fruit set nor carbohydrate levels in the

bark of one-year-old branches. Carbohydrate content could have been affected later than 15 DAFB, but no samples were taken after this time. Note that increases in carbohydrates in response to scoring have been detected 25 days or more after treatment (Kraybill, 1923). Because my goal was to study the possible effect of carbohydrate content on fruit set, and girdling had not affected set at the end of "June" drop, then carbohydrates were not analyzed at that stage, as previously planned. Scoring may not have been deep enough, as the treatment did not affect leaf color, size, or orientation, nor did it promote flowering the following year. Another possibility is that the cambium and bark recovered rapidly and the single cut was healed in a short period of time.

The lack of effect of 60% shade (significant only at $\alpha = 0.1$) and of girdling may have reflected the relatively high level of sorbitol in the cluster bases at full bloom (from 6.1 to 7.4% of dry wt.). Therefore, neither 60% shade (40% full sunlight, considered sufficient for normal growth and development) nor ringing was as effective as similar treatments applied in the second experiment, in which maximum sorbitol content of the cluster bases was 4.2%. Another factor to be considered is the natural light conditions during the spring of 1985; 3 to 4 consecutive days with a heavy overcast (<10% full sun) can markedly decrease fruit set in apple (Byers et al., 1990 b; Byers and Carbaugh, 1991; Lakso, 1984). In some cases limited

shading, e.g., 30% shade, alone or in combination with chemical thinning treatments (ethephon and carbaryl) can stimulate fruit abscission significantly (Lehman et al., 1987), but neither 30 nor 73% shade significantly reduced fruit set of non-chemically treated Starkrimson 'Delicious' apple trees. High solar radiation at Clarksville during the spring of 1985 could possible have reduced response to shading.

Experiment 2. 'Empire' and 'MacSpur'. In E. Lansing, MI, both shading (85 and 60% shade) and girdling significantly decreased initial and final set of 'Empire' and 'MacSpur' in 1985 (Table 4). "June" drop was negligible in this experiment. Shading (30%) before bloom did not affect carbohydrate levels in the flower cluster bases at full bloom or 7 days thereafter. However, 30% shade from bud break to full bloom, followed by 85% shade after petal fall practically eliminated all fruits (Table 4). Only 1 of the 4 trees treated set any fruits. This was expected, for the 85% shade covered the entire canopy and was kept on the trees continuously after petal fall. Similar results were reported by previous workers using 92% shade for 5 to 10 day periods (Byers, et al., 1990 a, b; Byers and Carbaugh, 1991; Byers et al., 1991; Polomski et al., 1988). The effect of 60% shade was less severe (Table 4), despite the fact that similar treatments had no effect on Redchief 'Delicious' in Experiment 1. Cultivar effects may account at least in part

for these differences, as suggested by the differences in response of 'MacSpur' vs. 'Empire' in 1986 (Table 4). Because the cultivars were planted in separate rows, the main plots (cultivars) could not be randomized, and cultivars were considered as blocks. Although block effect was not significant, a true test of cultivar differences was not possible. Differences in solar radiation between 1985 and 1986 could also have influenced response to shading, for cloudy weather reduces fruit set of apple (Byers and Carbaugh, 1991; Byers et al., 1991; Lakso, 1984).

Both shading treatments significantly reduced sorbitol, fructose, glucose and total water soluble carbohydrate content of the bark of one-year-old branches 25 days after full bloom, when initial fruit set was recorded (Table 7). Inositol in the bark was significantly reduced only by 85% shade, whereas sucrose levels were not affected by the treatments. Inositol levels were so low that even when differences between treatments were statistically significant, their biological significance was questionable. Although 85% shade was applied only after petal fall, the 60% shade treatment was applied continuously beginning at green tip to pink bud, yet no significant differences in carbohydrate content were observed either in cluster bases at FB or in the bark tissue at either FB or 7 DAFB (Tables 4 - 6). Therefore, the decrease in carbohydrate in bark tissue occurred during the period from 7 to 25 DAFB (Table 7). The data for the 60% shade treatment suggest that

photosynthetic activity is low in the early spring, and that early shoot growth and flowering are more dependent on previous year's carbohydrate reserves than has been assumed by some authors (Hansen, 1971 b; Hansen and Grausland, 1973).

My results on the effects of shading on carbohydrate content (sorbitol, fructose, glucose, and total water soluble carbohydrates) agree with those reported by Polomski et al. (1988). Furthermore, both fruitlets and bark tissue appear to be appropriate for measuring the effects of shading treatments on carbohydrates. Some quantitative differences might be expected, because growing fruitlets are usually the strongest sinks (Antoszewski and Lenz, 1982; Faust, 1989; Hansen, 1967, 1970 a, b, 1982). Therefore, higher amounts of photosynthates should be going to fruitlets than to the shoots (including the bark), which are weaker sinks (Faust, 1989).

Because of differences in plant material, intensity and timing of shading, portion of tree shaded, and analytical procedures used, quantitative comparison between data obtained by various workers is unwarranted. However, the carbohydrates analyzed and the tissue sampled deserve consideration. Sorbitol is the major photosynthate and transport carbohydrate in apple (Hansen, 1970 a, b; Sakai, 1966; Webb and Burley, 1962; Williams et al., 1967). It is readily transported throughout the tree, entering the flower or growing fruit, where it is transformed into sugars

(Williams et al., 1967), mainly sucrose, fructose, and glucose (Hansen, 1967, 1970 a). It also occurs in fruits from the earliest stages of fruit development until fruit maturity (Williams et al., 1967). Polomski et al. (1988) measured reducing and non-reducing sugars and starch (nonstructural carbohydrates), but not sorbitol. Thus the effects of shading and of terbacil on carbohydrate content may have been underestimated by the authors.

Another difficulty in using fruitlets as samples for studies relating to fruit set is that the apple fruitlets that eventually fall stop growing 10 or more days before fruit drop occurs (Polomski et al., 1988). Abscission is probably induced in such fruits before their growth rate declines. Sampling these small fruits may not give an accurate picture of the physiological causes of abscission, yet there is no good way to separate such fruits from those that persist. Finally, if a treatment prevents initial set, no fruits will be available for sampling.

On the other hand, when bark tissue of one-year-old branches is used, as in my study, detection of early differences in carbohydrates may be difficult. Since growing fruitlets are stronger sinks than are branches (Faust, 1989), and attract most of the photosynthates (Hansen, 1967, 1970 a), carbohydrate deficiencies may be detected earlier in the branches. In this case the bark tissue may be depleted of carbohydrates earlier than fruits. However, fruitlets may not be the strongest sinks under

stress caused by shading or other treatments which reduce photosynthesis. Apparently, the sink strength is reversed under such conditions; even when all fruits dropped, as in most of the 85% shade trees of this study, leaf abscission was negligible. However, carbohydrate content of the bark at 60 DAFB (20 to 25 days after the end of "June" drop) paralleled the effects of the treatments on fruit set (Table 8). The best procedure would be to use both fruitlet and bark samples; however, I used only bark.

Carbohydrate content of the cluster base should reflect that of the flower (and flower quality ?). Flower quality is an important factor in initial set. Goldwin (1989 a) suggested that lack of available carbohydrate might limit fruitlet growth, resulting in abscission. He (1989 b) treated 'Cox' flowers with the "Wye mixture" (GA3 + diphenylurea + naphthoxyacetic acid) to obtain parthenocarpic fruits. Some flowers responded by enlarging after anthesis; others did not. A rapid increase in dry matter content (about 35%) of the receptacle occurred in the first week in "good quality" flowers, whereas "poor quality" flowers failed to enlarge. Goldwin (1989 b) attributed this failure to either lack of carbohydrate or failure in the mechanism that leads to cell division. He suggested that the carbohydrates needed for the initial enlargement of the fruitlet are generated by photosynthesis within the flower itself, rather than being imported from the leaves, since little ¹⁴C was recovered from the flowers/fruitlets

following exposure of the spur leaves to ${}^{14}\text{CO}_2$ (Goldwin, 1985), and considerable 14C was detected in flowers exposed to 14CO2 (Goldwin, 1989 b). The significance of these results in normally pollinated (seeded) fruitlets is questionable, however, for hormone-induced parthenocarpic fruitlets all abscised when forced to compete with seeded fruitlets on the same tree (Goldwin, 1989 a). Therefore sink strength of hormone-induced fruitlets is weaker than that of seeded fruitlets. On the other hand, data obtained by other investigators indicate that large amounts (up to 90%) of the 14 C fixed can be transported to flowers and fruitlets from spur leaves exposed to 14 CO₂ (Hansen, 1967).

Regardless of the source of carbohydrates (reserves from previous season, import from spur and shoot leaves, or photosynthesis <u>in situ</u>), the data of experiment 1 with Redchief 'Delicious' (Table 1) show that set may not be reduced appreciably (significant only at p < 0.1) provided the carbohydrate content of the tissue is sufficiently high. In experiment 2, cluster bases of 'Empire' and 'MacSpur' contained 30 to 50% less carbohydrate than that of control trees, and set was significantly reduced by 60% shade (Table 4). Therefore, cluster base samples were appropriate indicators.

In order to induce greater fruitlet abscission by reducing carbohydrate levels, treatments must be applied within 25 DAFB. This is based on the observations of some authors that shade or photosynthetic inhibitors have maximum

effect in inducing abscission when applied from 10 to 25 DAFB (Polomski et al., 1988). Most flower and fruitlet abscission occurs 10 to 25 DAFB. This coincides with the stage when apple fruitlets can be chemically thinned (Greene, 1989).

Photosynthetic activity is increased in fruiting trees by increasing either sink size or sink activity (growing fruitlets are strong sinks), or both. If source size (leaf area) does not increase, the source activity (photosynthetic rate) must increase to maintain the source-sink relationship (Hansen, 1982). When fruits are thinned, sink size is reduced, carbohydrates accumulate in leaves, and the rate of photosynthesis decreases. Shading decreases source activity by restricting photosynthesis (Byers et al., 1990 b). Therefore heavy shade reduces carbohydrate availability to the growing fruitlets and stimulates fruitlet abscission. Chemical thinning agents may induce fruitlet abscission by interrupting transport of carbohydrates from leaves to fruitlets (Schneider, 1975, 1978 a, b). Shading (30 or 73%) of apple limbs for 16 days starting at petal fall significantly increased the thinning effect of a mixture of ethephon and carbaryl (Lehman et al., 1987). Therefore both fruit thinning chemicals and shade appear to act by affecting carbohydrate supply to fruitlets.

Based on these considerations, the significant reduction in carbohydrate caused by shading (experiment 2) probably was responsible for the marked decrease in fruit

set (Table 4). Furthermore, both responses paralleled the level of shade imposed. Therefore, carbohydrates appear to play an important role in fruit set of apple.

In contrast, the effect of girdling on fruit set appears to involve other factors. A deficiency of nitrogen may have been responsible for the negative effect of girdling on initial set (Table 4). Batjer and Westwood (1963) attributed the detrimental effect of girdling on fruit set to interference with the upward movement of nitrogen. Leaf nitrogen content affects both photosynthesis and fruit set (Faust, 1989). Photosynthesis increases with increasing leaf nitrogen content. However, part of the nitrogen absorbed is utilized in the roots, and carbohydrates are required for its metabolism. Therefore absorption is dependent upon photosynthetic activity (Faust, 1989). Trees were girdled at green tip, when photosynthesis was very limited, and leaves of girdled trees exhibited typical symptoms of nitrogen deficiency throughout the growing season. Therefore lack of nitrogen was probably responsible for reduced set. At 25 DAFB only glucose and starch were significantly higher in bark tissues of girdled trees than in those of control trees (Table 7).

The level of carbohydrates in bark of one-year-old branches at 60 DAFB does not appear to be related to fruit set, which had been determined 20 to 25 days earlier. However, these data (Table 8) may be better indicators of the effect of the treatments on carbohydrate content over a

longer period of time. In general, the effect of shading was similar to that in samples taken at 25 DAFB (Table 7). The carbohydrate levels remained lowest at 60 DAFB under 85% shade, followed by 60% shade. In the control trees levels of sorbitol, sucrose and starch continued to increase. Girdling induced the most marked increase in carbohydrates, mainly starch; however, glucose and fructose were also higher than in control trees. This clearly indicates that girdling increases carbohydrates in parts of the tree above the girdle. Given the erratic effects of girdling on set, more effort should be devoted to establishing the effects of timing and technique.

The correlation coefficients between final and initial fruit set were highly significant in both experiment 1 and experiment 2 (Tables 1 and 4), supporting the observation of Silva et al. (1980) that final set (crop load) is largely determined by number of flowers and initial set.

Both initial and final fruit set were significantly correlated with sucrose levels in the bark at 7 DAFB (Table 6, Figures 3 and 4), but not with levels in either cluster bases or bark at full bloom or in the bark at 25 DAFB. The significant correlations between both initial and final fruit set vs. levels of all carbohydrates, except inositol in the bark 60 DAFB, (Table 8, Figures 5-10) have little importance for the purpose of this study, given that fruit set had been established about 20 days prior to sampling. Shading reduced leaf specific dry weight (LSDW) (Table 9) in agreement with the data of Barden (1974, 1977), Lakso and Johnson (1982) and Marini and Barden (1982). LSDW increases with light intensity and is a function of leaf thickness (Wooge and Barden, 1987). Production of carbohydrates as well as their storage in, and transport out of, the leaves affects LSDW (Wooge and Barden, 1987).

Area of spur leaves was not affected by shading, but girdling significantly decreased the size of both spur and shoot leaves (Table 9). In contrast, leaf size on terminal shoots was increased by 60% shade, but not by 85% shade. Under heavy shade (85%), even leaf growth was reduced, whereas under 60% shade leaf area increased to compensate for the reduced rate of photosynthesis, as suggested by Hansen (1982). The decrease in leaf size on both spurs and terminal shoots of girdled trees again suggests interference with nutrient and water supply. As noted above, girdling may reduce upward movement of nitrogen (Batjer and Westwood, 1963). Photosynthetic activity declines for lack of nitrogen, and the roots use carbohydrates to metabolize nitrogen (Faust, 1989). Kraybill (1923) observed that girdling reduced nitrogen and also lowered moisture levels in apple shoots. Hansen (1982) suggested that girdling inhibits the growth of aerial portions of the tree by repressing root growth. A smaller root system absorbs less water and nutrients, thereby reducing the supply to the top.

Appropriate amounts of carbohydrates have to be available to flowers and fruitlets to assure both initial and final set, unless some detrimental effects from other factors occur.

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IV. FRUIT SET VS. CARBOHYDRATE CONTENT IN BARK AND CLUSTER BASE TISSUE OF APPLE: EFFECTS OF ROOTSTOCK, INTERSTEM, AND STRAIN.

Both rootstock and interstem reportedly affect fruit set of apple trees. In England, fruit set in 'Cox's Orange Pippin' trees was greater on the dwarfing rootstock M.9 than on more vigorous rootstocks (Blasco et al., 1982; Jackson et al., 1982 a). In the United States, fruit set of 'Delicious' was greater on the dwarfing rootstock MAC 9 than on more vigorous MAC clones such as MAC 11 and 24 (Dennis, 1981, b). The percentage of initial and final set of 'Cox's Orange Pippin' trees was greater in trees on the dwarfing rootstock M.9 EMLA, followed by trees that had a 15cm M.9 EMLA interstock, whereas the lowest fruit set was observed on the trees grafted directly on the vigorous rootstock M.111 (Webster et al., 1983).

In 'Delicious', differences among strains in setting ability have also been reported (Dennis, 1981 a, 1990). If carbohydrates play a role in the fruit setting ability of apple, rootstock, interstem and strain may influence set by affecting carbohydrate content of the tissues. Therefore, experiments were designed to determine the relationship between fruit set and level of sugars and starch in cluster base and bark tissues, using trees differing in rootstock, interstem and strain.

Materials and Methods.

Experiment 1. Effects of rootstock. To determine the effects of rootstock on fruit set and carbohydrate content, 'Imperial Red Delicious' trees propagated on three Michigan Apple Clone (MAC) rootstocks were used during 1985 and 1986. Trees on virus-indexed MAC 9 ('MARK'), MAC 11 or MAC 24 were planted at the Horticultural Teaching and Research Center (MSU), East Lansing, Michigan in 1970. Trees on MAC 9 were approximately 2.5 m in height; those on MAC 11 and 24 were approximately 5 m in height.

In 1985, 150 flower clusters on each experimental tree, distributed at random around the canopy at mid-height, were tagged and fruit set recorded; in 1986, 200 flower clusters per tree were tagged. In both years, only spurs on twoyear-old wood were used for fruit set observations and sampled for carbohydrate analysis. Cluster base samples were collected at full bloom in both years, whereas bark samples were taken at both full bloom (FB) and 15 days after FB in 1985, and at FB and 22 days after FB in 1986. Procedures of sampling, material preparation and carbohydrate analysis were as described in section 2 (Materials and Methods, general for all experiments). A completely randomized design with four replicates (trees) per treatment, was used.

Experiment 2. Effects of interstem. Eleven-year-old trees of 'Empire', planted at the Horticultural Teaching and Research Center (MSU), East Lansing, Michigan, were used to determine the influence of dwarfing interstem on fruit set vs. carbohydrate content of cluster bases and one-year-old bark tissues. In the spring of 1986, the following treatments were evaluated: 'Empire'/M.111; 'Empire'/M.8 (interstem)/M.111; and 'Empire'/M.9 (interstem)/M.111. Tree height was approximately 4, 2, 2.5 m, respectively. The trees were arranged in a randomized complete block design with four replications (blocks) per treatment and one tree per plot. A minimum of 100 flower clusters on spurs on twoyear-old wood, distributed at random around the middle height of the canopy, were tagged at full bloom. Cluster bases (20 per tree) were sampled from those tagged flowering limbs at this time. Bark samples (15 discs, 8mm in diameter) were collected from one-year-old terminal shoots on the tagged limbs both at full bloom and at 23 days after full bloom. Fruitlets on tagged spurs were counted at petal fall and again after "June" drop and initial and final fruit set was calculated. Details about sampling procedure, material preparation, and carbohydrate analysis are described in section 2 (Material and Methods, general for all the experiments).

Experiment 3. Effects of 'Delicious' strain and rootstock. In the spring of 1985, fruit set in trees of six strains of 'Delicious' was recorded and samples were taken for carbohydrate analysis. The trees were part of an experiment comparing 28 strains of 'Delicious' apple on both M.7 and M.111, planted in 1980 at Clarksville Horticultural Research Station, Clarksville, Michigan. Three strains that had the highest fruit set in 1984 (Improved Ryan Red, Apex, and Sturdeespur), and three strains that had the lowest fruit set (Rose Red, Spured Royal, and Nured Royal), were compared. Cluster bases and bark tissue were both sampled at full bloom, and analyzed for sorbitol, fructose, glucose, sucrose, inositol, and starch. Cluster bases (20 per tree) were sampled from trees on both M.7 and M.111 rootstock, while bark was sampled only from trees on M.7. Both cluster base and bark samples were taken at random around the periphery of the canopy. One representative limb per tree was tagged at full bloom and the flowers were counted. At 25 DAFB and again after "June" drop, the fruitlets were counted and initial and final fruit set were calculated. Procedures of sampling, material preparation, carbohydrate extraction and analysis are described in section 2 (Material and Methods, general section for all the experiments).

Results

Experiment 1. Effects of rootstock. Trees on 'Mark' (MAC 9) had higher fruit set than trees on either MAC 11 or MAC 24, whereas the difference between MAC 11 and MAC 24 was non-significant (Table 10). Rootstock affected the level of sorbitol, fructose, and glucose in cluster bases, but differences in other carbohydrates were non-significant (Table 10). Differences between MAC 9 and MAC 11 were nonsignificant. Correlation coefficients across all rootstocks indicated that final fruit set was positively correlated with levels of sorbitol, sucrose and total water soluble sugars, whereas other r values were non-significant (Table 10, Figures 13 - 15).

Starch was higher in bark of trees at FB on MAC 24 than in that of trees on either MAC 9 or MAC 11 (Table 10). Correlation coefficients across all rootstocks indicated no significant relationship between fruit set and level of carbohydrates in the bark at full bloom (Table 10).

Rootstock did not significantly affect carbohydrates in bark tissue at 15 days after full bloom, nor were correlation coefficients between final set and level of each carbohydrate significant (Table 10).

When the experiment was repeated in 1986, fruit set appeared to be greater on MAC 9, but differences were not significant (Table 11). Fructose, glucose, and sucrose were significantly lower in cluster bases of trees on MAC 11 than

in those on either of the other two rootstocks. Correlation coefficients between fruit set and levels of each carbohydrate, calculated across rootstocks, were not significant (Table 11).

No effects of rootstock on levels of sugars or starch in bark tissue of one-year-old branches sampled at either date were significant and correlation coefficients were also non-significant.

Experiment 2. Effects of interstem. Use of either interstem increased both initial and final set (Table 12). Only fructose levels were significantly affected by interstem, both interstems increasing the concentration in cluster bases. Both initial and final set were positively correlated with level of fructose (Table 12, Figures 17 and 18), whereas no significant relationships with other carbohydrates were found. Final fruit set was also significantly correlated with initial fruit set (Table 12, Figure 16).

In bark tissue, sorbitol was the only carbohydrate to be affected by interstem at full bloom, trees with interstems having higher levels (Table 12). All correlations between either initial or final fruit set and levels of carbohydrates of bark at FB were non-significant. Analysis of samples taken at 23 DAFB indicated no significant effects of interstem, but starch level was
positively correlated with final fruit set (Table 12, Figure 19).

Experiment 3. Effects of 'Delicious' strain and rootstock. Fruit set differed from expected, in that the more productive strains (Improved Ryan Red, Apex, and Sturdeespur) were not clearly separated from the less productive ones (Rose Red, Spured Royal, and Nured Royal), although final set was highest in Sturdeespur and lowest in Nured Royal (Table 13). Sturdeespur, Spured Royal and Nured Royal had relatively high initial set. However, final set was significantly higher on M.7 than on M.111. Nured Royal, Rose Red and Spured Royal had similar levels of sorbitol, all of which were consistently higher than in the other three strains (Table 13). Similarly these three strains contained higher levels of fructose and glucose than did Apex and Sturdeespur. Improved Ryan Red was intermediate in fructose content, but higher in glucose than Apex and Sturdeespur. Apex had higher level of starch in the cluster bases than all other strains except Strudeespur. Starch content of Sturdeespur was similar to that of Spured Royal, but significantly higher than that of the remaining three strains.

Correlation coefficients between final set and initial set were significant, but neither initial set nor final set were correlated with carbohydrate content (Table 13, Figures 20 and 21).

Bark carbohydrates were analyzed only in trees on M.7. Despite the low value for final set of Nured Royal, no strain effects were significant except for higher levels of starch in Rose Red (Table 13). Initial set was not correlated with carbohydrate content; however, significant positive correlations were evident in final fruit set vs. a) initial set and b) levels of fructose and glucose of bark (Table 13, Figures 22 and 23).

	Final Fruit set (%)	Carbohydrates (% dry weight)									
Rootstock		Water Soluble Carbohydrates									
		Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total				
		Cluster base									
MAC 9	21.38a ^y	4.70a	0.36a	0.62a	0.03	1.01	6.72a	0.26			
MAC 11	10.706	3.72ab	0.36a	0.60a	0.04	0.87	5.59a	0.28			
MAC 24	8.70b	2 .39 b	0.14b	0.29b	0.03	0.72	3.57ь	0.25			
۲ ^Z		0.710**	0.418ns	0.450ns	-0.217ns	0.702*	0.698*	-0.004			
(final set vi carbohydrate	content)										
		Bark at full bloom									
MAC 9		1.65	0.53	0.73	0.02	0.42	3.35b	0.19Ь			
MAC 11		2.74	0.86	1.28	0.02	0.56	5.468	0.216			
MAC 24		2.21	0.62	0.88	0.02	0.59	4.32ab	0.30a			
r		-0.301ns	-0.278ns	-0.296ns	-0.199ns	-0.432ns	-0.313ns	-0.481m			
(final set v	8										
carbohydrate	content)										
		Bark at 15 days after full bloom									
MAC Q		4.1 8	1.02	1.38	0.05	0.85	7.48	0.49			
MAC 11		3.99	1.09	1.43	0.05	0.26	6.82	0.64			
MAC 24		3.97	1.04	1.28	0.03	0.74	7.06	0.55			
r		0.021ns	-0.528ns	-0.213ns	0.332ns	-0.010ns	-0.053ns	-0.055n			
(final set va carbohydrate	s content)										

Table 10. Effects of rootstock on fruit set and carbohydrate levels of flower cluster bases and bark of one-year-old branches of 'Imperial Red Delicious' apple trees. Horticultural Teaching and Research Center, E. Lansing, NI 1985.

² r value required for significance with 10 df = 0.576 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .

** = Significant at p < 0.01; ns = non significant at p < 0.05.

. . //w Final Fruit Set)

F



Figure 13. Correlation between final fruit set (% of flowers) and levels of sorbitol in the cluster bases of 'Imperial Red Delicious' apple trees on different MAC rootstocks at full bloom. East Lansing, MI. 1985.



Figure 14. Correlation between final fruit set (% of flowers) and levels of sucrose in the cluster bases of 'Imperial Red Delicious' apple trees at full bloom. East Lansing, MI. 1985.



Figure 15. Correlation between final fruit set (% of flowers) and levels of total water soluble carbohydrates in the cluster bases of 'Imperial Red Delicious' apple trees at full bloom. East Lansing, MI. 1986.

Table 11. Effects of rootstock on fruit set and carbohydrate levels of flower cluster bases and bark of one-year-old branches of 'Imperial Red Delicious' apple trees. Horticultural Teaching and Research Center, E. Lansing, MI 1986.

	Final Fruit set (%)	Carbohydrates (% dry weight)								
		Water Soluble Carbohvdrates								
Rootstock		Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total			
		Cluster base								
MAC 9	21.75	1.96	0.23a ^y	0.27a	0.13	2.10a	4.69	0.62		
MAC 11	15.11	2.96	0.13b	0.15Ь	0.07	1.106	4.41	0.52		
MAC 24	15.48	1.52	0.22a	0.24 a	0.08	2.32a	4.39	0.57		
۲Z		0.155ns	0.188ns	0.264ns	0.365ns	0.185ns	0.552ns	0.408n		
(final set vs										
carbohydrate c	ontent)									
		Bark at full bloom								
MAC 9		3.57	0.45	0.72	0.04	1.16	5.94	0.24		
MAC 11		3.12	0.54	0.79	0.05	1.17	5.67	0.10		
MAC 24		2.89	0.56	0.85	0.04	0.93	5.27	0.20		
r		-0.212ns	-0.333ns	-0.510ns	-0.060ns	-0.157ns	-0.251ns	0.131n		
(final set vs										
carbohydrate c	ontent)									
		Bark at 22 days after full bloom								
MAC 9		4.18	0.68	0.94	0.09	0.48	7.00	0.32		
MAC 11		4.39	0.68	0.95	0.11	0.37	6.50	0.38		
MAC 24		4.60	0.68	0.92	0.09	0.33	6.62	0.56		
r		0.085ns	0.010ns	-0.212ns	0.154ns	0.440ns	0.206ns	-0.441n		
(final set vs										
carbohydrate c	ontent)									
Y Nean separat	ion within col	ume by DMR	 t n < 0.05	•••••	•••••		•••••	••••••		

fruit set were transformed to arcsin \sqrt{x} .

** = Significant at p < 0.01; ns = non significant at p < 0.05.

_____ Carbohydrates (% dry weight) -----Interstem/ Fruit set (%) Water Soluble Carbohydrates Starch Rootstock Initial Final Sorbitol Fructose Glucose Inositol Sucrose Total Cluster base -----26.4a^y 23.9a 0.11 M.8 / M.111 2.47 0.15a 0.06 0.18 2.97Ъ 0.49 M.9 / H.111 24.7a 21.9a 2.76 0.17a 0.13 0.07 0.33 3.468 0.46 17.7b 14.0b 2.50 0.09b 0.08 M.111 0.06 0.30 3.04b 0.49 ٢Z 0.080ns 0.653* 0.384ns -0.246ns -0.187ns 0.051ns -0.017ns (initial set vs carbohydrate content) 0.891** 0.733** r 0.134ns 0.569ns 0.023ns -0.120ns 0.146ns -0.007ns (final set vs initial set or carbohydrate content) Bark at full bloom -----M.8 / M.111 2.27ь 0.11 0.22 0.02 0.78 3.406 0.14 N.9 / M.111 0.22 0.32 0.03 1.06 4.27a 0.12 2.64a M.111 2.206 0.16 0.23 0.03 0.95 0.12 3.57b 0.269ns 0.105ns 0.128ns -0.054ns 0.094ns 0.200ns 0.030ns г (initial set vs carbohydrate content) 0.362ns 0.019ns 0.120ns -0.112ns 0.093ns 0.240ns -0.016ns r (final set vs carbohydrate content) _____ Bark at 23 days after full bloom M.8 / M.111 3.77 0.53 0.55 0.06 0.37 5.28 1.39 0.04 M.9 / M.111 2.75 0.43 0.46 0.17 3.85 1.64 0.21 0.06 3.73 0.84 2.87 0.31 0.28 M.111 0.065ns 0.148ns 0.408ns -0.193ns -0.425ns 0.356ns 0.409ns r (initial set vs carbohydrate content) 0.162ns 0.408ns 0.575ns -0.289ns 0.362ns 0.239ns 0.581 r (final set vs carbohydrate content) _____

Table 12. Effects of interstem on fruit set and carbohydrate levels of flower cluster bases and bark of one-year-old branches of 'Empire' apple trees. Horticultural Teaching and Research Center, E. Lansing, MI 1986.

Y Hean separation within columns by DMRT, p < 0.05.

² r value required for significance with 10 df = 0.576 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .

** = Significant at p < 0.01; ns = non significant at p < 0.05.

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Figure 16. Correlation between final and initial fruit set (% of flowers) of 'Empire' apple trees on different interstems. East Lansing, MI. 1986.



Figure 17. Correlation between initial fruit set (% of flowers) and levels of fructose in the cluster bases of 'Empire' apple trees on different interstems at full bloom. East Lansing, MI. 1986.



Figure 18. Correlation between final fruit set (% of flowers) and levels of fructose in the cluster bases of 'Empire' apple trees on different interstems at full bloom. East Lansing, MI. 1986.



Figure 19. Correlation between final fruit set (% of flowers) and levels of starch in the bark of one-year-old branches of 'Empire' apple trees on different interstems at 23 DAFB. East Lansing, MI. 1986.

				0	.	()	L			
	Carbohydrates (% dry weight)									
train/	Fruit set (%)					Starch				
ootstock	Initial	Final	Sorbitol	Fructose	Glucose	Inositol	Sucrose	Total		
				Clus	ter bases	• M.7 and M.	 111			
ose Red	55.3ab ^X	14.1c	5.14a	0.22a	0.53a	0.10	0.22	6.21a	0.27c	
pured Royal	55.1ab	18.9ab	4.85a	0.22a	0.52 a	0.08	0.22	5 .89a	0.51bc	
ured Royal	43.5bc	9.1d	5.28a	0.24a	0.73 a	0.10	0.17	6.52 a	0.37c	
mproved	48.6bc	14.8bc	3.55b	0.15 a b	0.72a	0.06	0.13	4.61b	0.32c	
Ryan Red										
pex	40.5c	16.5bc	2.67c	0.08b	0.12Ь	0.08	0.16	3.11c	0.76a	
turdeespur	63.9a	22.6a	2.94bc	0.11b	0.10b	0.02	0.10	3.27c	0.72at	
у			-0.236ns	-0.260ns	0.010ns	-0.081ns	0.082ns	-0.195ns	-0.058r	
initial set vs										
arbohydrate lev	els)									
1	0.600*	*	-0.330ns	-0.353ns	-0.091ns	-0.088ns	0.089ns	-0.249ns	0.0941	
final set vs										
nitial set or										
arbohydrate lev	els)									
ootstock										
.7	46.6	17.1	4.23	0.15	0.46	0.06	0.16	5.06	0.48	
.111	55.7	14.9	3.91	0.19	0.45	0.09	0.18	4.82	0.50	
0.05	08	*	05	DE	D £	08	DS	DE	08	
••••										
				Bark -	N.7 only					
ose Red	45.0	13.6	2.50	0.25	0.37	0.02	1.13	4.27	0.62a	
pured Royal	44.1	19.1	2.51	0.25	0.39	0.02	0.38	3.55	0.44b	
ured Royal	39.2	6.3	2.50	0.27	0.43	0.02	1.07	4.29	0.38b	
mproved	50.2	16.4	2.17	0.27	0.34	0.01	1.11	3.90	0.43b	
Ryan Red										
pex	42.8	20.2	2.18	0.35	0.49	0.01	0.53	3.56	0.39Ь	
turdeespur	58.4	26.8	2.21	0.35	0.53	0.01	0.96	3.97	0.41b	
z			-0.332ns	0.484ns	0.383ns	-0.192ns	0.115ns	0.097ns	0.137	
initial set vs										
arbohydrate lev	els)									
-	0.765*		-0.411ns	0.751**	0.665*	-0.352ns	-0.123ns	-0.022ns	-0.534	
final set vs										
nitial set or										
	ele)									

² r value required for significance with 10 df = 0.576 (p < 0.05). Data in percentage of initial and final fruit set were transformed to arcsin \sqrt{x} .

*; **; ns: significant at p < 0.05; p < 0.01; and non-significant at p < 0.05, respectively.

Table 13. Effects of rootstock and strain of 'Delicious' apple on fruit set and carbohydrate content in



Figure 20. Correlation between final and initial fruit set (% of flowers) of six strains of 'Delicious' on M.7 and M.111 rootstocks. Clarksville, MI. 1985.



Figure 21. Correlation between final and initial fruit set (% of flowers) of six strains of 'Delicious' on M.7 only. Clarksville, MI. 1985.



Figure 22. Correlation between final fruit set (% of flowers) and levels of fructose in the bark of one-year-old branches of six strains of 'Delicious' on M.7 rootstock at full bloom. Clarksville, MI. 1985.



Figure 23. Correlation between final fruit set (% of flowers) and levels of glucose in the bark of one-year-old branches of six strains of 'Delicious' on M.7 rootstock at full bloom. Clarksville, MI. 1985.

Discussion

Experiment 1. Effects of rootstock. The higher fruit set of trees of 'Imperial Red Delicious' on MAC 9 (Table 10) confirmed that apple trees on dwarf rootstocks set more fruits or have higher yield efficiency than trees on semivigorous or vigorous rootstocks (Carlson and Tukey, 1959; Dennis, 1979, 1981 a, b). The higher levels of sorbitol, fructose, glucose, and total water soluble sugars in cluster bases of trees on MAC 9 relative to MAC 24 paralleled the differences in fruit set. However, the carbohydrate levels in trees on MAC 11, which also had lower fruit set than trees on MAC 9, did not differ significantly from the levels in the MAC 9. Therefore, the relationship between carbohydrate content and fruit set did not hold across all three rootstocks.

The positive significant correlation between final fruit set and levels of sorbitol, sucrose, and total water soluble carbohydrate (Table 10; Figures 13, 14, 15) may indicate that carbohydrate content in cluster bases is related to fruit set. Sorbitol and sucrose are considered to be the two major photosynthates produced and transported in apple (Webb and Burley, 1962; Whetter and Taper, 1963; Williams and Raese, 1974). Therefore, differences between setting ability of apple trees on different rootstocks do not appear to be due to differences in carbohydrate content of cluster bases; however sorbitol, sucrose and total water

soluble sugar levels of cluster bases may still be important for fruit set.

Carbohydrate content of bark tissue at full bloom did not parallel that of cluster bases (Table 10). The lower level of total soluble sugars in bark of trees on MAC 9 suggests that the flowers may be more effective in mobilizing carbohydrates when MAC 9 is used as a rootstock than when either MAC 11 or MAC 24 is used. Hansen (1982) suggested that apple rootstocks can affect assimilation and utilization of carbohydrate. Maidebura et al. (1978) observed that apple trees on the dwarf rootstock M.9 had higher photosynthetic productivity than did trees on semidwarfing or vigorous rootstocks. Leaves of 'Jonathan' apple trees on M.9 had higher chlorophyll content and photosynthesis than leaves of trees of the same cultivar on the semi-vigorous to vigorous rootstock M.4 (Rud et al., 1978 a, b). Higher photosynthetic productivity was also observed in apple trees on the dwarfing rootstock Budagovski Paradise than in trees of the same cultivars on seedling or semi-vigorous rootstocks (Trunov and Muromtsev, 1982).

Highest utilization of assimilates in an apple tree occurs during flowering and fruit set, when respiration rate is high (Khormenko, 1978). Levels of reducing sugars in the flowers, primarily in the petals, are also very high during bloom (Howlett, 1926). The flowers of trees on MAC 9 may have had a higher sink strength than those on trees on the other rootstocks, for sorbitol, sucrose, total water soluble

carbohydrates, and starch tended to be higher in the former (Table 10). This could lead to better flower "quality" and better set, as suggested by Goldwin (1989 a, b).

Carbohydrate content of the bark generally increased between bloom and 15 DAFB; this increase was greater in trees on MAC 9 than on other rootstocks. For example, sorbitol increased 153% in trees on MAC 9, but only 45 and 80%, respectively, in those on MAC 11 and MAC 24 (Table 10). Similar values for water-soluble carbohydrates are 123 vs. 25 and 63%, this despite the heavier fruit set on MAC 9. The critical period for stimulating fruit abscission by shading or treatment with terbacil is between 10 and 25 DAFB (Byers et al., 1990 b; Polomski et al., 1988). Flowers and fruitlets on trees with MAC 9 rootstocks may have had a better carbohydrate supply during that critical period than those on either of the other stocks.

Although the data for fruit set obtained in 1986 paralleled those obtained in 1985, the differences between rootstocks were non-significant (Table 11). Rootstock effects were neither significant in cluster bases and bark, nor was fruit set significantly correlated with levels of any of the carbohydrates. The fruits were not thinned in 1985, therefore fruit density was considerably greater in trees on MAC 9 than in those on MAC 11 or MAC 24. This could have reduced carbohydrate content more in the cluster bases in trees on MAC 9 in 1986 relative to those on other stocks. Grochowska (1973) observed that starch content of

spurs was reduced by fruiting, and this difference was significant until 18 weeks after full bloom. However, she did not continue sampling thereafter. Although Buszard (1983) found starch content of apple flower buds to be significantly lower in fruiting than in non-fruiting spurs until September, differences in October were nonsignificant. However, non-fruiting trees had flower buds with larger diameter which had higher initial and final set than flower buds of heavily cropping trees.

Experiment 2. Effects of interstem. The importance of initial fruit set on final fruit set was evident in this experiment (Table 12, Figure 16). Similar results have been observed by several authors, both for hormone-induced parthenocarpic apple fruits (Buszard and Schwabe, 1989; Goldwin, 1989 a, b) and for pollinated fruits (Buszard and Schwabe, 1989; Silva et al., 1980).

Dwarfing interstem can increase initial or final fruit set of 'Empire' trees compared to trees grafted directly on M.111 (Table 12). Trees with interstems were less vigorous, and this may have favored fruit production. The fructose content of cluster bases was also higher in trees with interstems. Although trees with M.9 interstems had higher total water soluble carbohydrates in the cluster bases and bark, and higher sorbitol in the bark, than did those grafted directly on M.111, trees with M.8 interstems did not

differ significantly from those on M.111 in these respects (Table 12).

Correlation coefficients indicated that initial and final set were correlated with fructose content of the cluster bases, but not of the bark (Table 12, Figures 17 and 18). Thus fructose content of the cluster bases was more closely associated with fruit set than was the content of other carbohydrates.

The results of this experiment indicate that the M.9 interstem increases carbohydrate content of the cluster base more than does the M.8 interstem, although both are dwarfing. Trees on M.8 interstem were smaller than those on M.9 (data not shown); thus the effect upon scion growth is not necessarily associated with effect upon carbohydrate content of the scion. However, more observations are necessary before definite conclusions can be drawn. Apple trees on dwarfing or semi-dwarfing rootstocks generally have higher yield and/or yield efficiency than do those on vigorous rootstocks, but exceptions do occur (Carlson and Perry, 1986; Schechter et al., 1991; Warrington et al., 1990). The scion cultivar and the length of the interstem can also influence efficiency (Carlson and Oh, 1975). Similarly, cropping efficiency can be affected by strainrootstock interaction (Dennis, 1988, 1990). None of these authors measured carbohydrate content, however. Furthermore, most authors who publish yield records do not

report data for fruit set or flower density, both of which may affect yield efficiency.

Dwarfing rootstocks can affect chlorophyll content and photosynthesis in apple leaves. Both chlorophyll content and leaf photosynthesis was higher in 'Jonathan' leaves on M.9 than on M.4 rootstocks (Rud et al., 1978 a, b). Sevento-nine-year-old trees on M.9 had higher photosynthetic activity than did trees on semi-dwarfing or vigorous rootstocks (Maidebura et al., 1978). Trees on the dwarfing rootstock Budagovski Paradise (BP) had higher photosynthetic efficiency than did trees on vigorous seedlings of <u>Malus</u> prunifolia (Trunov and Muromtsev, 1982).

Apple flowers are strong sinks (Hansen, 1971 b), and two-thirds or more of the reducing carbohydrates in the flower at bloom are in the petals (Howlett, 1926). The small but significant increases in fructose content of cluster bases of trees observed with M.8 or M.9 interstems may underestimate the actual differences in the flowers. Starch content of the bark increased much more from full bloom to 23 DAFB in interstem trees than in trees without interstems. This may indicate that they also had higher photosynthetic rates during this period. Although there were no significant differences between treatments in starch content at any sampling date, final set was positively correlated with starch content at 23 DAFB (Table 13, Figure 19). Thus dwarfing interstems may affect fruit set by increasing the

availability of carbohydrates to flowers and growing fruitlets.

Experiment 3. Effects of 'Delicious' strain and rootstock. Strain can affect both initial and final fruit set, while rootstock has a small but initial effect on final set only (Table 13). Final set from highest to lowest, was Sturdeespur ≥ Spured Royal ≥ Apex = Improved Ryan Red = Rose Red > Nured Royal. In the previous year, Rose Red, Spured Royal and Nured Royal set a significantly smaller proportion of flowers than did Improved Ryan Red, Apex, and Sturdeespur (number of fruits per 100 flower clusters were 12, 52, 9, 8, 46, and 63, respectively). Sorbitol, fructose, glucose, total water-soluble carbohydrates, and starch were consistently higher, with but one exception, in cluster bases of Rose Red, Spured Royal, and Nured Royal than in Apex and Sturdeespur. Levels in Improved Ryan Red were generally intermediate between these two groups (Table 13). No observed differences in bark tissue, except for starch, among strains, was probably because samples were taken only from trees on M.7 rootstock (2 replicates per strain), and only Rose Red differed from the other strains in starch content.

Only two r values for percent fruit set vs. carbohydrate content were significant (p < 0.05) in either cluster bases or bark, these being for fructose and glucose in the bark (both positive, Table 13, Figures 22 and 23).

Sturdeespur was one of the most productive strains among 28 tested at Clarksville, MI, and among 23 compared at Kearneysville, WV (Warrington et al., 1990). In the same trials, Nured Royal had significantly lower yield efficiency than Spured Royal, Sturdeespur, Apex, and Rose Red, whereas yield of Improved Ryan Red was similar to Nured Royal.

Based on my data, differences in carbohydrate levels in cluster bases and bark tissue at full bloom cannot explain the differences in fruit setting ability among strains. Only fructose content appeared to be positively correlated with set. Therefore, other factors probably determine the fruitsetting ability of these strains. Such factors could include ovule longevity and effective pollination period, photosynthetic efficiency, sink strength, and rate of transport of carbohydrates, etc.

The higher final set in trees on M.7 rootstock (Table 13) agrees with previous reports on this trial (Dennis, 1988, 1990). However, rootstock effects on levels of carbohydrates in the bark of the scions were nonsignificant.

Positive relationships between final and initial fruit set were observed when both rootstocks M.7 and M.111 were considered, and when data of trees on M.7 only were used (Table 13, Figures 22 and 23). Then, the importance of initial fruit set was also evident in this experiment as has been suggested by several researchers (Buszard, 1983;

Buszard and Schwabe, 1989; Goldwin 1989 a, b; Silva et al., 1980).

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V. FRUIT SET VS. CARBOHYDRATE LEVELS IN BARK AND CLUSTER BASES IN COMMERCIAL ORCHARDS.

Heavy cropping can reduce apple fruit set the following year in comparison with trees that bear few or no fruits (Buszard, 1983). Urea sprays applied in the spring can increase fruit set in the current season (Stainer, 1986); similar treatment during the summer or fall can increase apple fruit set the following season (Hill-Cottingham and Williams, 1967; Stainer, 1986). Carbohydrates may be involved in the setting ability of apple trees, since factors that favor photosynthesis or carbohydrate accumulation or availability can increase fruit set. Solar radiation from previous to flower opening until five days after flowering was positively correlated with fruit set of 'Delicious' tree (Dennis, 1981 c). On the other hand, partial shading or defoliation can decrease fruit set of apple (Byers et al., 1985, 1990 a, b; Doud and Ferree, 1980; Faby and Naumann, 1986; Lehman et al., 1987; Polomski et al., 1988; Schneider, 1975, 1978 a, b; Schumacher et al., 1987). Some authors suggest that carbohydrate production, or availability to flowers and developing fruitlets, controls fruit set (Buszard, 1983; Byers et al., 1990 a, b; Faby and Naumann, 1986; Ferree and Cahoon, 1987; Polomski et al., 1988; Reich, 1985; Salzer, 1982; Schneider, 1975, 1978 a; Schumacher et al., 1987; Siebertz and Lenz, 1982;

Treccani et al., 1982). If this hypothesis is correct, assuming that bees and viable pollen are available differences in fruit set should be paralleled by differences in carbohydrate level. To study this aspect, data were collected for fruit set and carbohydrate content in trees of Starkrimson 'Delicious' apple on seedling rootstock in four commercial apple orchards in Central Michigan.

Materials and Methods

Four commercial orchards of Starkrimson 'Delicious'/seedling were selected in Central Michigan in the fall of 1984. None of the orchards required thinning in 1984, since none had excessive loads. In each orchard, 7 trees of uniform size were selected while still dormant. Three well-exposed limbs were tagged on each tree and their diameter measured at the base (5 to 10 cm of cross-section). Five bark discs from one-year-old terminal branches and 8 cluster bases were taken from each limb at full bloom. Procedures of sampling, material preparation and carbohydrate analysis are described in detail in section 2 -Materials and Methods, general section. The number of clusters and flowers on the tagged limbs were then counted. Fruitlets remaining were counted 53 days after full bloom

Basal limb cross-sectional area was calculated and flower density was expressed as number of flowers per cm^2 .

Correlation coefficients were calculated for fruit set vs. levels of sugars and starch.

Results

Although flower density was higher in orchard 2 than in the other 3 orchards, final fruit set was highest in orchard 3 (Table 14). Sorbitol concentration in both cluster base and bark, and water soluble sugar concentrations in cluster bases were also higher in orchard 3 than in the other orchards. Water soluble sugar content in bark tissue was higher in orchard 3 than in orchards 1 and 2, but did not significantly differ from that of trees in orchard 4. Carbohydrates other than starch were generally lowest in the cluster bases in orchard 4. Final fruit set was positively correlated with levels of carbohydrates other than starch in cluster bases, but correlations between fruit set and levels of carbohydrates in the bark were not significant. The levels of carbohydrates, except for fructose and starch, in bark tissue were the highest or among the highest in orchard Starch was higher in the bark of trees of orchard 1, 3. whereas no significant differences in starch content in the bark tissue among the other orchards were observed.

Table 14. Comparison of fruit set and carbohydrate levels in cluster bases and in bark of one-year-old branches of Starkrimson 'Delicious' apple in four orchards in Michigan (1985). Carbohydrates (% dry weight) -----Fruit Flower Fruit /cm² limb /cm² limb Sorbitol Fructose Glucose Inositol Sucrose Water Soluble Starch /100 Orchard flowers cross-sec cross-sec Carbohydrates -----Cluster base 1. Belding, MI 23.3b^y 28.3b 2.03b 0.12a 0.16a 0.04b 6.8 0.18b 2.53b 0.27ab 22.2b 55.7a 2. Lowell, MI 12.4 1.34c 0.09ab 0.15a 0.10a 0.23b 1.91c 0.28a 3. Belding, MI 37.9a 25.3b 10.1 3.29a 0.11a 0.18a 0.12a 0.38a 4.08a 0.24b 4. Lowell, MI 15.5b 38.9b 6.6 1.19c 0.06b 0.08b 0.05b 0.06c 1.44c 0.26ab ۳Z -0.164ns 0.637** 0.599** 0.439* 0.415* 0.412* 0.570** 0.584** -0.268ns (final set vs flower density, fruit density or carbohydrate content) Bark 2.70c 0.73 0.98a 0.03b 0.77 5.21c 1. Belding, MI 0.42 0.23b 0.71 0.79Ь 0.02Ь 0.98 5.47bc 2. Lowell, MI 2.97bc 3. Belding, MI 3.40a 0.88 1.11a 0.06a 0.63 6.08a 0.23b 3.085 0.94 1.05a 0.07a 0.73 5.87ab 0.185 4. Lowell, MI 0.201ns -0.042ns 0.173ns 0.021ns -0.072ns 0.137ns 0.165ns (final set vs carbohydrate content) _____

^y Mean separation within columns by DMRT, p < 0.05.

² r value required for significance with 26 df = 0.374 (p < 0.05). Data in percentage of final fruit set were transformed to arcsin $\sqrt{3}$.

 $*_{z}$ **; ns: significant at p < 0.05; p < 0.01; and non-significant at p < 0.05, respectively.



Figure 24. Correlation between final fruit set (% of flowers) and levels of sorbitol in the cluster bases of Starkrimson 'Delicious' apple in 4 Michigan orchards at full bloom in 1985.


Figure 25. Correlation between final fruit set (% of flowers) and levels of fructose in the cluster bases of Starkrimson 'Delicious' apple in 4 Michigan orchards at full bloom in 1985.



Figure 26. Correlation between final fruit set (% of flowers) and levels of glucose in the cluster bases of Starkrimson 'Delicious' apple in 4 Michigan orchards at full bloom in 1985.



Figure 27. Correlation between final fruit set (% of flowers) and levels of inositol in the cluster bases of Starkrimson 'Delicious' apple in 4 Michigan orchards at full bloom in 1985.



Figure 28. Correlation between final fruit set (% of flowers) and levels of sucrose in the cluster bases of Starkrimson 'Delicious' apple in 4 Michigan orchards at full bloom in 1985

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Figure 29. Correlation between final fruit set (% of flowers) and levels of total water soluble carbohydrates in the cluster bases of Starkrimson 'Delicious' apple in 4 Michigan orchards at full bloom in 1985.

Discussion

The negative correlation coefficient between final fruit set and flower density was not significant (Table 14). The antagonistic effect of flower density on fruit set that has been suggested by several authors (Heinicke, 1917; see also Dennis, 1979; 1984) was not apparent. However, a minimum threshold in flower density may be required for this relationship to be observed. Differences in yield efficiency per limb (fruit/cm² limb cross-section) were not significant. Only 3 limbs (5-10 cm² cross-sectional area each) were used per mature tree on seedling rootstock. On these large trees, small differences in fruit/cm² limb cross-section could reflect great differences in total fruit crop per tree.

The higher fruit set in trees of orchard 3 was associated with higher carbohydrate content, mainly sorbitol, sucrose and total water soluble carbohydrates, in the cluster base (Table 14, Figures 24 - 29). Starch was lower in cluster bases of trees of orchard 3 than in those of orchard 2, but was not significantly different from those in orchards 1 and 4 (Table 14).

Trees of orchard 3 also had higher sorbitol in bark tissues, while levels of glucose, inositol, and total water soluble carbohydrates were as high or higher than that in the other orchards (Table 14). On the other hand, trees of

orchard 1 had higher starch content in the bark than did trees in the other orchards.

Fruit set was significantly correlated with soluble carbohydrates in cluster bases, but not with starch or any of the carbohydrates in the bark.

The reasons for the higher levels of soluble carbohydrates in orchard 3 are not known. However, several factors can be ruled out. Training and pruning of the trees, which can influence light and possibly photosynthesis inside the canopy (Cain, 1971, 1972; Jackson, 1980; Porpiglia and Barden, 1981), were similar among orchards. Fruit load in the previous year, which could have affected flower quality and carbohydrate reserves (Buszard, 1983; Buszard and Schwabe, 1989; Goldwin, 1989 a, b; Grochowska, 1973; Schaefer and Scharz, 1986; Siebertz and Lenz, 1982), was not heavy, for none of the orchards needed fruit thinning in 1984. Climatic conditions that can affect pollination, fertilization and fruit set, such as temperature, light, wind, rain, or frost during flowering and fruit setting (Ballard et al., 1971; Byers and Carbaugh, 1991; Brittain, 1933; Dennis, 1979, 1981 c; Lakso, 1984; Lapins and Arndt, 1974) were quite uniform. Pesticide treatments during bloom may affect pollen germination and bee activity in pollination (Stainer, 1986), but in Michigan apple growers use similar treatments.

Nutrient content was not measured. Orchard 3 was the only orchard in which animal manure had been applied. This

could have increased N content, favoring photosynthesis both during the previous year (1984), as well as in the spring of 1985, when this study was performed. Increasing the level of N in the leaves can increase photosynthesis and carbohydrate availability to flowers and fruitlets (Barbarosh, 1978; Faust, 1989; Rud et al., 1978 a, b).

The differences in carbohydrate content in cluster bases suggest that carbohydrates are important for flower quality and fruit set, as mentioned by several authors (Goldwin, 1989 a, b; Lakso, 1984; Lakso et al., 1984; Schneider, 1975, 1978 a, b). However, the content of carbohydrate in the bark did not appear to be a good indication of the carbohydrate status of the cluster bases.

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The levels of sorbitol in cluster bases were low in comparison with levels in previous experiments, in which much younger trees were used. For example, levels of sorbitol in cluster bases of Redchief 'Delicious'/M.7 EMLA trees were all higher than 6% of dry weight (Table 1). Old trees produce more fruit relative to vegetative growth than do young trees (Faust, 1989; Kriedemann, 1982). This reduces the amount of carbohydrate available for flowering and fruit set (Schaefer and Scharz, 1986; Siebertz and Lenz, 1982).

The result of this study definitely implicates carbohydrate availability to flowers and growing fruitlets as being important to fruit set of mature apple trees.

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VI. SUMMARY AND CONCLUSIONS

Relative effects of all experiments and treatments are summarized in Table 15. Values for treated trees (shade, girdling) are compared with those for controls (no treatment), or one treatment (rootstock, strain, orchard) is taken as a "standard" treatment for comparison with others. Symbols (+, -, 0) indicate higher, lower, or similar values, respectively, relative to those of controls/standards, and asterisks indicate statistically significant differences (p < 0.05).

Part III. The only treatment that reduced set (at p < 0.10) was shading in both fall and spring. Although 60 % shade reduced mean values for carbohydrate content of Redchief 'Delicious' in all but 3 comparisons (Exp. 1), none of these differences was significant at p < 0.05, and only 3 were significant at p < 0.10 (Table 16). Thirty per cent shade and scoring were even less effective.

Shading of 'Empire' and 'MacSpur' trees (Exp. 2) markedly reduced both initial (recorded 25 DAFB) and final set. Carbohydrate content of the bark was not affected at 7 DAFB, but was reduced significantly at 25 days after bloom. Thus depletion of carbohydrates between 7 and 25 DAFB could be responsible for reduced set. Girdling reduced set, but carbohydrate content was not affected. Thus although the effects of shading support the hypothesis that carbohydrate

content determines set, the effects of girdling do not. However, girdling appeared to induce N deficiency, which may in turn have reduced set.

Part IV. Trees on MAC 9 rootstocks set a higher percentage of their flowers in 1985 than did those on MAC 11 or MAC 24 (Table 16). Similar differences were observed in 1986, but were not statistically significant. Carbohydrate content of cluster bases was generally lower with both MAC 11 and MAC 24 than with MAC 9. Differences in bark samples were inconsistent and generally non- significant. Thus the effect of rootstock on carbohydrate content did not consistently parallel the effect on set.

Use of M.8 and M.9 interstems increased set relative to no interstem (Table 16). Values for carbohydrate content in cluster bases and bark of trees on M.9 interstem were usually higher than those for trees without interstems, although the differences were seldom significant. In contrast, the M.8 interstem had no consistent effect. Carbohydrate content may therefore be responsible for the effect of the M.9 interstem on set, but cannot explain the effect of M.8.

No "control" was used in the 'Delicious' strain experiment, therefore the strain with the highest set (Sturdeespur) was taken as the standard. Four strains set significantly fewer fruits than did Sturdeespur, and soluble carbohydrate content of the cluster bases was usually higher, rather than lower, than in Sturdeespur. Therefore, no correlation can be claimed.

Part V. Orchards 1, 2, and 4 set significantly less fruit than did Orchard 3, and content of carbohydrates other than starch was lower in these orchards than in Orchard 3 in most comparisons. Thus carbohydrate content may have affected set. Mature trees were used in this experiment, whereas young trees (5 to 11 years old) were used in all other comparisons. Carbohydrates could be more important for fruit set in mature trees than in young trees. If this were true, one would expect lower levels of carbohydrates in old than in young trees. My data for total soluble carbohydrates for control and standard trees in Parts III and IV are compared with those for the trees used in Part V in Table 16.

Carbohydrate levels in the cluster bases of mature trees were relatively low in comparison with those in young trees, but the values overlapped. In contrast, levels in the bark were relatively high in comparison with young trees. Based upon these limited data, the suggestion that carbohydrates are more important in mature than in young trees does not appear to be warranted.

In summary, my data, taken as a whole, do not support the hypothesis that carbohydrates in the cluster base and bark at bloom and shortly thereafter are crucial for initial fruit set. Other factors, possibly hormones synthesized in

the leaf or the rootstock, may interact with carbohydrates in determining set.

Discretation Part	Treatment	Fruit Set 🕱	Cluste	r Bases a	(Full B	nom		Bark a	t Full Bl	om / 15	-25 DAF	æ	
Cultivar			Sor	Fru . G	lu Su	Tot	Sla	Sor	<u>F</u>	ole G	Suc	Tot	Sta
III. Exp 1	None ²	20.3				•							
Redchief	S-F (60%)	20.9 -	•	•	•	•	•	÷	÷	÷	÷	÷	÷
'Delicious'	S-S (60%)	14.1 -7	•	•	•	•	•	K - -	÷		+/+	÷	÷
1084-1985	S-S (30%)	19.9 .	+	•	•	+	•	÷	0/0	+-	·+	+/+	÷
	Scorine	20.8	•	0 0	•	•	•	+;-	+-	+-	·'+	+;	· • •
Frn 2	None ²	15.35								•		•	
- des - entre		0.11.0	•	.+ +	•	•	•	•;-	•	•	÷	÷	·/+
cmpire		- 07 -	•	• •	+	•	•	•-/+	•-/+	·/+	.)0	•+	-++
IORG MACOPUL	o-s Cirdline	9.75	•	• + • +	+	•	•	÷	+;	•+-	+	+;-	+ +
v. Fra l	MAC 9 ²	21.38		•									
Dellelour	MAC 11	10.70 .	•	c	•	•	+	· +	+/+	+/+	· + ·	·· +	+/+
1985	MAC 24	8.70	•.	•.	•	•.	•	·/+	+/+	÷	·/+	· +	+ - +
	MAC 9 ²	21.75											
1086	MACII	15.11 .	+	•.	•.	۰.	•	+/•	8 +	+/+	·/+	÷	+;
	MAC 24	15.48 -	•	•	+	•	•	+;-	۹ +	·+	÷	÷	+;
f j	M.1112	14.0											
	M AM III	23.9 +	•	+ •+	•	•	0						
			4	•	+	•+	•						
1 780	M.7/M.111		-	•	-	•							
Exp J			•	•	•	4			Frelud	d heese	a of limi	ted replic	ations.
Delicious	spured Koyal	+	F	⊢	⊦ 4	⊦,	, 4						
strains on	Apet		•	•	•		+•						
M.7 & M.III	Improved Ryan Red	14.8	+	+ +	+	+	. •						
1985	Ross Red	14.1	+	+	+	+	•••						
	Nured Royal	- 1.6	•	+ •	+	+	•.						
	Orchard 32	37.9											
	1		•.	•	•.	۰.	+	•,	•	•	+	•.	•+
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Delicious			•	•	•	•		•	4		• •	•.	•
1985	Orchand 4	• • • •	•	•	•	•	F	,	۰.	,	-		

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² Treatment used for comparison with all other treatments in the same experiment Y Significantly different from the standard treatment at the p < 0.05 level ° Significantly different from the standard treatment at the p < 0.10 level Abbreviations: S-F = Shading during fall; S-S = Shading during spring

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Part	Experiment	Year	Total soluble carb	ohydrate (% d.w.)
			cluster bases	bark
III	1	1984-85	8.65	6.75
	2	1986	5.12	4.15
IV	1	1985	6.72	3.35
		1986	4.69	4.41
	2	1986	2.97	3.04
	3	1985	3.27	3.97
vz	-	1985	1.44-4.08	5.21-6.08

\$1.

Table 16. Total soluble carbohydrates in cluster bases and bark of control and standard trees (see Table 15) at full bloom.

^Z Range for 4 orchards of mature trees.

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