PHOTOSYNTHATE PRODUCTION AND PARTITIONING IN APPLE LEAVES

by

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(ABSTRACT)

Mature field-grown apple trees were used to gain a better understanding of the influences of light and fruit on leaf physiology. Light effects on net photosynthesis (Pn), specific leaf weight (SLW), leaf N content (weight/area)(N_W), and leaf N concentration (% dry weight)(N_P) of spur leaves from two canopy locations were evaluated on four dates in 1987. Interior leaves had lower Pn, SLW, N_W, and N_P than exterior leaves. In 1988 the influence of % available photosynthetic photon flux (PPF) on the same parameters was examined throughout the season. On most measurement dates both Pn and SLW increased quadratically while N_W increased linearly with increasing PPF. In both years positive linear relationships existed between Pn and N_W, SLW and N_W, and Pn and SLW.

Photosynthate production and partitioning as influenced by fruit and girdling was studied in 1986 by selecting pairs of fruiting and nonfruiting spurs on two cultivars and girdling one of each pair. With both cultivars, at 7 days after treatment (DAT) leaves on girdled-nonfruiting spurs had the lowest Pn while Pn of girdled-fruiting and nongirdled (±fruit) spurs did not differ. At 7 DAT leaves on girdled-nonfruiting spurs had the highest SLW, girdled-fruiting the lowest, and nongirdled (±fruit) were intermediate. In 1988, fruiting spurs with various leaf to fruit ratios and comparable nonfruiting spurs on two cultivars were girdled. An interaction between fruiting status and time existed for most parameters measured on both cultivars. At 1 DAT few differences existed due to fruiting status. At 8 DAT Pn, transpiration (Tr), and nonreducing sugars were greater while leaf resistance (R_L), SLW, and starch were lower on fruiting than nonfruiting spurs. In nonfruiting spurs Pn and Tr tended to decrease while R_L and SLW increased with time. Total nonstructural carbohydrates, reducing sugars, and starch were lower in fruiting than nonfruiting spurs. These studies indicated that SLW was a simple and reliable indicator of canopy light environments and that the influence of fruit on leaf physiology includes modification of leaf carbohydrate contents. Fruiting status did not influence Pn except on girdled spurs where Pn was higher with fruit than without fruit.

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Chapter 1

Introduction

Production practices in U.S. orchards are being modified to accommodate changing economic pressures. Increasing costs, particularly for land and labor, are causing the low tree density plantings of the past to give way to new high-density orchards. The use of size controlling rootstocks has been a very important factor in this transition. However, even with these rootstocks satisfactory size control is not always obtained and continual adjustments to cultural practices are often necessary.

Failure to properly manage a high density planting can rapidly cause the advantages of this growing system to become problems. For example, the benefit of rapid development of the tree canopy and resulting earlier returns on investment can become a drawback if the canopy cannot be maintained at the proper size. Canopy density is also important as light is a critical factor in the production of high quality fruit. If the canopy becomes too dense, yield from the inner areas of the canopy is reduced, both in volume and quality. Because of these factors, high-density orchards require more intensive management than do conventional systems.

Research evaluation of new and modified production systems often focuses on fruit yield and quality. This procedure has the disadvantage of requiring several growing seasons in order to obtain results. Another method of system evaluation is measurement of light levels within the canopy. With apple researchers have found that specific leaf weight (SLW) is a useful indicator of the previous light environment of a leaf (Barden, 1978; Marini and Barden, 1981). This type of canopy evaluation is easier and less expensive than light measurements. Recently, it has been reported that leaf nitrogen (N) content is also related to light exposure (DeJong and Doyle, 1985; Weinbaum et al., 1989).

The ideal situation in an orchard would be to have rapid tree growth until the trees fill their allotted space and thereafter have most of the fixed carbon allocated to fruit production. Bearing trees produce less vegetative growth but more total dry matter than comparable nonfruiting trees (Avery, 1969, 1970; Maggs, 1963). Although many theories exist as to the physiological basis for this observation, we still do not totally understand the physiological processes regulating carbohydrate production and partitioning. Regulating these processes could theoretically increase yield by favoring partitioning to the fruit. The potential decrease in vegetative growth would also have numerous benefits including reduced pruning costs, control of tree size, and improved light penetration into the canopy interior.

Productivity of a tree is ultimately dependent upon carbon assimilation. Since factors affecting net photosynthesis (Pn) would be expected to affect yield, Pn is frequently used to evaluate tree productivity. A greater understanding of physiological factors regulating Pn in apple would allow growers to provide optimal conditions for carbon assimilation resulting in maximum yield efficiency. The objectives of this study with apple were:

1. To define the relationships between light exposure, SLW, Pn, and leaf N content.

2. To quantify the effect of fruit on gas exchange, stomatal conductance, water potential, carbohydrate production, and carbohydrate constituents of adjacent leaves.

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Literature Review

General

Fruit production is dependent upon many factors including cultivar/rootstock combination, planting system, pruning method, and general management practices. On a more basic level, however, yield is dependent upon maximum light interception, efficient conversion of light energy into carbohydrates, and subsequent partitioning of carbohydrates to the various tree components. Of these three basic factors, light interception is probably the most important as carbohydrate production is dependent upon light interception.

Jackson (1978) stated that high light interception is necessary for maximum yield since radiant energy reaching the orchard floor doesn't contribute to fruit production. In a later review article he also noted the importance of optimizing both light distribution within the tree canopy and light interception by different parts of the canopy (Jackson, 1980). Optimal light utilization would result in the greatest rates of both Pn and fruit growth, maximize flower bud formation, and optimize fruit quality.

Total light exposure is not necessary for every fruiting spur in order to obtain maximum yields. Shading apple trees down to light levels of 45% full sunlight did not decrease flower bud production (Jackson, 1975). Researchers working with high-coloring strains of 'Delicious' reported no increase in % red skin color of fruit with increasing light exposures from levels as low as 5 to 9% PAR (Barritt et al., 1987; Robinson et al., 1983). However, low-coloring cultivars such as 'McIntosh' need light levels of at least 40% PAR for commercially acceptable color development (Lakso, 1980).

Light effects on leaf physiology

Net photosynthesis (Pn) in apple leaves increases hyperbolically in response to increasing light levels (Barden, 1971, 1977; Lakso and Seeley, 1978; Proctor et al., 1976). Mika and Antoszewski (1972) and Heinicke (1966) reported that Pn rates of peripheral leaves of an apple tree were three to four times higher than leaves from the inner canopy. Previous research reported that light levels decreased as foliage depth increased (Heinicke, 1963, 1964) and Mika and Antoszewski (1972) and Heinicke (1966) attributed the lower Pn rates of the interior leaves to insufficient light exposure. More recent studies of leaves from the inner canopy have established that Pn of these leaves was reduced even at saturating light levels (Barden, 1974, 1977; Marini and Barden, 1981; Porpiglia and Barden, 1980).

Examination of the morphological features of a leaf that may affect Pn began in the 1930's. Pickett (1934) studied the internal structure of leaves of two cultivars of apple collected from trees grown under both field and greenhouse conditions. He then related his observations to estimated Pn of these leaves (as determined by diurnal changes in SLW and carbohydrate content). Although there were variations in Pn due to cultivar, the differences due to tree location (orchard vs. greenhouse) were greater. He concluded that the higher rates of Pn in orchard-grown trees were a result of the increased amount of intercellular spaces in leaves from those trees. He had earlier proposed that the amount of intercellular space could be an important factor affecting Pn (Pickett, 1933) and in a later study reported that it was more important than leaf chlorophyll content (Pickett and Kenworthy, 1939).

Apple leaf structure varied both with position upon a shoot and type of growth (shoot vs. spur) (Cowart, 1935). Along a shoot, leaf thickness decreased from the base to the middle and then increased to the apex. Leaf area increased from the base to the middle and then decreased to the apex. However, the percent of the lamina occupied by palisade cells increased from the base to the apex. Generally, the palisade cells became more elongate and the palisade layers were more compact and well defined as leaf position approached the apex. Shoot leaves were thicker and larger than comparable spur leaves.

Although implied in some of the studies cited previously, the effect of light exposure on leaf structure was not discussed. Auchter et al. (1926) reported that shading increased leaf size, decreased leaf thickness, and changed the structure of a leaf. Using light levels of 100, 78, 41, and 24% full sun, Maggs (1960) demonstrated that reduced light increased leaf size and internal gas space while it decreased lamina thickness. A linear relationship between apple leaf thickness and light intensity was reported by Jackson and Beakbane (1970). They suggested that variations in leaf thickness may be used to measure variations in light climate if used with a few actual light measurements.

Concurrent with the discussion of decreased leaf thickness with increased shading in these studies was the observation that SLW was also affected. Apple leaves from long shoots had both more highly developed palisade parenchyma and higher SLW than spur leaves presumably because the former were exposed to higher light levels (Ghosh 1973). Avery (1977) reported that leaves from both greenhouse-grown and shaded trees had lower SLW and were thinner than trees exposed to full sun; Maggs (1960) had previously observed that leaves from low-light conditions had increased specific area (area/weight). The effects of leaf structure on Pn were measured in some of these studies but the variations in light levels and methods make it difficult to draw any clear conclusions.

Apple leaf Pn and SLW were affected by the light environment a leaf was in when it unfolded; leaves unfolding under low-light conditions had lower values for both parameters (Barden, 1974). Even after a leaf was fully expanded, changes in the light environment still altered both Pn and SLW. It was proposed that SLW may be a useful index of both previous light exposure and Pn potential of a leaf. In a later study examining the effects of continuous and intermittent shade on apple tree growth, a positive relationship between Pn and SLW was reported (Barden, 1977). Using data from both studies it was found that between 26 and 82% of the variation in Pn could be explained by SLW with an average of about 55% (Barden, 1978). Again it was suggested that SLW could be a useful index of previous light environments because of its ease of determination. Studies conducted concurrently and more recently have also reported a relationship between SLW and light exposure in apple

(Avery, 1975a; Barritt et al., 1987; Doud and Ferree, 1980; Jackson and Palmer, 1977) as well as peach (DeJong and Doyle, 1985; Kappel and Flore, 1983; Marini and Marini, 1983), walnut (Erez and Weinbaum, 1985; Klein et al., 1989), citrus (Syvertsen and Smith, 1984), and prune (Weinbaum et al., 1989).

In a seasonal evaluation of canopy development, Porpiglia and Barden (1980) found that the Pn potential of apple spur leaves from the canopy exterior remained relatively constant while rates of those from the interior tended to decrease. SLW, however, tended to increase throughout the season at all canopy locations. A linear relationship existed between Pn and SLW in apple from May through August (Marini and Barden, 1981). As Pn rates declined in September, the nature of the relationship became quadratic and by October it was linear again but with lower correlation coefficients. Based on these data it was concluded that SLW would only be a useful predictor of Pn through mid-season. However, SLW still appeared to be a reliable index of the previous light environment of a leaf.

A relationship between Pn and SLW has also been reported in other crops. Marini and Marini (1983) reported a linear correlation between these two factors in peach in both June and August with the relationship being stronger in August. They concluded that SLW was a reasonably good indicator of Pn through mid-August. In a later study comparing light exposure in a pruned vs. an unpruned peach tree DeJong and Doyle (1985) reported a curvilinear relationship between Pn and SLW. These researchers did not examine the relationship throughout the season or make any statements regarding the use of SLW to predict Pn. Although both Pn and SLW varied directly with light level in citrus, no attempt was made to relate the two variables or to use SLW to predict Pn (Syvertsen, 1984; Syvertsen and Smith, 1984).

Working with soybeans, Dornhoff and Shibles (1970) reported that Pn was correlated with SLW and proposed that SLW may be a useful index for the selection of soybeans with higher Pn rates. In alfalfa Pn and SLW were also correlated and again it was suggested that plant selection for increased yield could be based on SLW (Pearce et al., 1969). A later study with soybeans also found a relationship between SLW and Pn but noted that the relationship held only for comparing plants grown under the same light source. (Bowes et al., 1972).

A late season application of nitrogen (N) to an apple tree kept its leaves dark green longer and enabled the tree to maintain higher rates of Pn (up to 124%) than on a comparable unfertilized tree (Heinicke, 1934). Trees grown without N had Pn rates 33% of those given a complete nutrient solution (Childers and Cowart, 1935). The role of N in Pn specifically in relation to N deficiency has been reviewed (Barker, 1979; Natr, 1972) and will not be discussed here. However, recent studies have found differences in Pn as affected by leaf N content in plants that have adequate N nutrition.

Ishii and Nagai (1981) reported a linear relationship between Pn and leaf N content (on a % dry weight (DW) basis). Similar relationships have been reported in Eucalyptus (Mooney et al., 1978), chaparral shrub (Gulmon and Chu, 1981), and soybean (Lugg and Sinclair, 1981). A strong linear relationship between Pn and N content (weight/-area) has been found in peach (DeJong, 1982, 1983) and four other Prunus species (DeJong, 1983) and a similar relationship has been reported in citrus (Syvertsen, 1987).

Two papers published in 1983 discussed the hypothesis that leaf N was allocated for maximum efficiency of carbon gain. Field (1983) used a biochemically-based model to predict the optimal leaf N distribution to maximize Pn. The model predicted that the highest N concentrations would exist in microsites receiving the highest daily PAR. Actual data with Lepechinia calycina, a chaparral shrub, supported this hypothesis. At low PAR leaf N content had little effect on Pn. Increasing leaf N at sites receiving low daily PAR would not increase Pn and would not result in higher net carbon gain by the plant. He noted that older leaves usually have both lower N content and lower daily PAR exposure reflecting the plants' redistribution of N for maximum carbon gain. The second study supported the first observing that as leaves age N is removed and leaf function responds to that removal while maintaining resource-use efficiency (Field and Mooney, 1983).

DeJong and Doyle (1985) examined the seasonal relationships between leaf N (weight/area) and light exposure in peach tree canopies to test the concept of optimization of leaf N. Leaf N was correlated with light exposure throughout the season with the strongest correlations existing in late June and July. SLW was also correlated with light exposure throughout the season but the correlation coefficients were lower than those of leaf N. The slope of the lines for the relationship between leaf N and light exposure became steeper during the season implying that N was being redistributed and supporting the hypothesis of N distribution for maximum carbon gain. A recent study with prune has reported similar results (Weinbaum et al., 1989).

Earlier studies had reported a variation in leaf N concentration with canopy position. Koo and Sites (1956) observed leaves from the outer canopy in citrus had a higher % N than those from the inner canopy in the summer flush of growth. Leaf N content (weight/area) was higher in the upper canopy of 'Golden Delicious' than in the middle or lower canopy positions (Haynes and Goh 1980). The differences were not as pronounced in 'Granny Smith' and this observation was attributed to light exposure. The canopy of 'Granny Smith' was more open and thus there would be a more uniform distribution of light throughout the canopy. Leaf N content was also lower in leaves of apple trees in high density plantings where there was more competition for light (Barrera-Guerra and Slowik, 1980).

Nitrogen content of peach leaves on a % DW basis decreased throughout the season while it remained relatively constant when calculated as mg/leaf (McClung and Lott, 1956). Leaf dry weight increased throughout the season and it was concluded that this factor was responsible for the downward trend on a % DW basis as the N was "diluted". The same trend has also been observed in apple (Rogers et al., 1953). Often the effect of light on N content of a leaf (wt/area) appears to be an indirect effect of higher SLW values for leaves exposed to greater amounts of light. Examples of this effect, no differences in

% N on a DW basis but differences on a weight/area basis as affected by light exposure, have been reported in walnut (Erez and Weinbaum, 1985; Klein et al., 1989) and prune (Weinbaum et al., 1989). Leaf N content on an area basis has been positively correlated with SLW in both citrus (Syvertsen and Smith, 1984) and peach (DeJong and Doyle, 1985).

Fruit effects on leaf physiology

Chandler and Heinicke (1926) reported that fruiting apple trees produced more dry matter per unit leaf area than equivalent nonfruiting trees. The possible explanations for this observation were a.) Pn in the skin of the fruit b.) more rapid Pn for a given leaf area and c.) reduced losses of carbohydrates due to removal of the fruit (wood remaining on the tree would presumably continue to respire). A later study reported similar results with apple grown at locations in both California and New York (Chandler 1934).

Maggs (1963) reported a reduction in both vegetative and root growth of cropping trees. However, he noted increased total dry matter production by the cropping trees and attributed this to increased removal rates of the photosynthates from the leaves. Similar results have been reported by Avery (1969, 1970). In later studies, Maggs (1964, 1965) observed that partially defoliated apple trees had comparable growth to control trees. He noted that photosynthetic efficiency of the remaining foliage must have been enhanced and concluded that leaves are generally functioning at levels below their maximum Pn potential.

Pn rates of apple leaves were highest in leaves closest to fruit and then decreased with increasing distance from the fruit (Kazaryan et al., 1965). Pn rates varied from 12.6 mg $CO_2/dm^2/hr$ on leaves nearest fruit to 5.7 on a nonfruiting branch. Ghosh (1973) also reported that the presence of fruit stimulated apple leaf Pn. Leaves on fruiting shoots and spurs had Pn rates 1 to 3 mg $CO_2/dm^2/hr$ higher than leaves on nonfruiting shoots and spurs. Hansen (1970) observed that the uptake of $^{14}CO_2$ was 1.5 times greater by leaves on fruiting shoots compared to nonfruiting shoots. In earlier studies he had noted a more rapid translocation of ^{14}C out of leaves closest to fruit (Hansen, 1967, 1969) and predicted that this would affect Pn of those leaves.

The presence of fruit has also been reported to affect Pn in peach. Crews et al. (1975) observed that highest Pn rates were in leaves closest to fruit (12.5 mg $CO_2/dm^2/hr$) with decreasing rates (down to 10) as distance from the fruit increased. This effect, however, was only observed during the third stage of fruit development when the fruits would be placing their maximum carbohydrate demand on the tree. Chalmers et al. (1975) also reported increased Pn during the final stage of fruit development. In this latter experiment the increase in Pn is reported as a whole-tree effect rather than as a specific leaf to fruit relationship. Pn rates averaged below 8 mg $CO_2/dm^2/hr$ which is lower than rates reported by Crews et al. (1975).

Monselise and Lenz (1980b) also reported a whole-tree effect of fruiting on Pn of apple. Using virtually the entire canopy of two-year-old potted trees, they measured increased Pn rates on fruiting compared to deblossomed trees. They also noted that the fruiting trees produced more total dry matter and concluded that this was a result of the increased sink strength of the fruit. Measurements were made in mid- to late August. Fujii and Kennedy (1985) followed apple leaf Pn throughout the season using excised limbs and measuring Pn in the lab. They reported increased Pn in fruiting trees during two periods of the growing season. The first was during bloom and the second was during the period of rapid fruit growth from July to September.

Not all studies have measured a fruit effect on Pn. While determining the effects of paclobutrazol, a growth regulator, on Pn and growth of nectarine, DeJong and Doyle (1984) did not measure increased Pn during the final stage of fruit development. They noted that in earlier studies where a fruit effect was reported (Chalmers et al., 1975; Crews et al., 1975) Pn rates were much lower than in their study and hypothesized that the observed fruiting effect may have been a reversal of a stress-induced inhibition of Pn. DeJong (1986) then conducted a study to determine the seasonal effects of fruit on Pn in peach. Comparing defruited and unthinned trees he measured increased Pn on the latter during June and July. There was no fruit effect on Pn in May or any residual effects in a post-harvest measurement in August. He noted that the magnitude of the observed fruit effect was lower than had been reported earlier on peach (Chalmers et al., 1975; Crews et al., 1975). This fruit effect was also much lower than the 45-60% increase in Pn of apple that Avery (1975b), after reviewing the literature, concluded was induced by fruiting. DeJong stated that the reduced fruit effect on Pn he observed may have been a result of the development of alternate sinks on the defruited trees due to favorable environmental conditions.

There are also reports of no measurable effect of fruiting on Pn in apple. In a study examining the role of spur leaves and bourse shoots in fruit set and development, Ferree and Palmer (1982) examined the influence of fruit on spur leaf Pn. Measurements were made on spurs with zero, one, two, or three fruit in July and no differences in Pn were observed. Later studies by Rom and Ferree (1986a, 1986b) reported no effect of fruit on spur leaf Pn. They noted that differences in fruiting condition of the trees used (fruiting and nonfruiting spurs on fruiting trees vs. fruiting or nonfruiting trees) and differences in methodology (excised vs. attached spurs and/or shoots) may have caused the discrepancies in findings of previous studies.

The time of Pn measurement is also important. Pn was higher on fruiting apple trees than nonfruiting trees at midday (Rom, 1987). Nonfruiting trees had maximum Pn two hours after sunrise while fruiting trees did not attain maximum Pn until four hours after sunrise. Hansen (1970) reported little if any difference in the uptake of $^{14}CO_2$ by fruiting vs. nonfruiting apple shoots shortly after a dark period; later in the day fruiting shoots often had 1.5 times the rate of uptake of nonfruiting shoots. In a recent review article, Flore and Lakso (1989) discussed the factors which may lead to the inconsistency in measuring a fruit effect on Pn.

The presence of fruit can affect SLW. Avery (1975b) reported that leaves not associated with fruit had higher SLW and explained this observation as a potential accumulation of carbohydrates in these leaves. Barritt et al. (1987) made similar observations and indicated that this supports the concept of fruit as a strong sink. Earlier Hansen (1967) reported that the translocation of ^{14}C out of leaves was enhanced in fruiting shoots. Monselise and Lenz (1980a) observed that as few as 10 fruit on a four-year-old apple tree were sufficient to cause a reduction in SLW compared to a deblossomed tree. Recently, a study to examine the effect of fruit removal on Pn and SLW of avocado leaves indicated that at 14 and 28 days after fruit removal SLW was 25% greater while Pn was 40-50% lower on girdled branches with no fruit (Schaffer et al., 1987). At 14 days after fruit removal, the average number of starch grains per microscope field was greater in leaves of the defruited branches than in those with fruit and it was concluded that this increase in starch acted as a feedback mechanism inhibiting Pn.

The increase in SLW on nonfruiting spurs or shoots is apparently not beneficial. Schaffer et al. (1987) observed no differences in the thickness or morphology of leaves from fruiting or nonfruiting shoots. As a result they concluded that the measured increase in SLW was strictly a result of carbohydrates accumulating in the leaves. Unlike the research of Barden (1974, 1977, 1978) where higher SLW implied higher Pn potential, higher SLW of leaves associated with a nonfruiting status implies Pn rates below the potential of leaves associated with fruit.

Some effects of fruiting on carbohydrate production and partitioning have been examined in strawberry. Forney and Breen (1985), using deblossomed and fruiting day-neutral plants, measured up to 44% greater SLW as well as increased starch content of crown, leaf blades, and roots of nonfruiting plants. They also measured Pn rates 60-80% higher in cropping plants during fruit development. Although total plant dry weight was the same throughout the study, fruiting plants had lower dry weight accumulation in roots, crown, and leaves. The researchers concluded that strawberry fruit inhibit starch accumulation and growth of vegetative tissues while maintaining or enhancing Pn. Similar results were reported from a later study with both day-neutral and June-bearing strawberry cultivars. During fruit maturation SLW was again higher in deblossomed plants (Schaffer et al., 1986a). Pn of a leaf that unfolded during bloom did not differ from that of a comparable leaf on a deblossomed plant while a newly expanded leaf on a fruiting plant did have higher Pn during weeks five and six of the second fruiting cycle of the day-neutral plants. Deblossomed plants had greater leaf and root dry weights than fruiting plants while total dry matter production did not differ between the plant types. At the end of the first fruiting cycle the roots of nonfruiting day-neutral plants had a higher percentage of total nonstructural carbohydrates (TNC) than roots of fruiting plants. Leaf carbohydrates were not measured.

A study examining the effect of fruiting on whole plant Pn and carbohydrate partitioning in strawberry showed no differences in whole plant dry weight at any time over the course of the study (Schaffer et al., 1986b). However, at the end of the fruiting cycle, dry weight and TNC content of the leaves were higher on deblossomed plants than fruiting plants. Pn was higher for deblossomed plants on a whole plant basis during the last three weeks of a six week fruiting cycle. Although it was mentioned that Pn was correlated with TNC on three of the six measurement days, there is no explanation of the nature of the relationship.

The hypothesis that Pn is controlled by assimilate concentrations in the leaf has been reviewed by several authors (Daie, 1985; Geiger, 1976; Gifford and Evans, 1981; Herold, 1980; Neales and Incoll, 1968). In apple leaves sorbitol is the dominant sugar followed by sucrose, glucose, and fructose (Chong and Taper, 1971; Loescher et al., 1982; Taper and Liu, 1969; Whetter and Taper, 1963). In a diurnal evaluation of carbohydrates in apple leaves from June through October, starch concentrations were similar to sucrose concentrations (Chong and Taper, 1971). During June, July, and August sorbitol concentrations in the leaves reached a peak in mid-to-late afternoon. Since apple Pn is at a maximum rate about midday and decreases throughout the afternoon (Landsburg et al., 1975), the increased concentration of sorbitol in the leaves later in the day would support the carbohydrate feedback inhibition of Pn theory.

Apple leaf transpiration followed the same diurnal pattern as Pn (Landsburg et al., 1975). In peach this relationship was observed throughout the season and increased Pn on fruiting trees was generally associated with higher rates of transpiration, although the maximum and minimum rates of both processes did not correspond exactly (Chalmers et al., 1983). Fujii and Kennedy (1985) did not observe differences in transpiration rates between fruiting and nonfruiting apple spurs. They did, however, report higher Pn in fruiting than nonfruiting spurs for two separate periods during the growing season. The results of these two studies imply the presence of nonstomatal limitations on Pn.

As with transpiration, the effects of fruiting on stomatal conductance (or resistance) are not consistent. No differences in leaf resistance between fruiting and nonfruiting apple spurs were observed in either field or laboratory measurements from May through November (Fujii and Kennedy, 1985). Fruit removal from mature apple trees did not result in drastic changes in stomatal conductance in either of two measurement years (Proctor, 1981). Measurements comparing leaf conductance on fruiting, deblossomed, and defruited apple trees were different on two of three measurement dates but it was noted that these differences were rarely greater than 20% (Jones and Cumming, 1984).

There are, however, some reports of more distinct effects of fruiting on stomatal conductance. Monselise and Lenz (1980a), comparing deblossomed and unthinned potted apple, reported stomatal resistance measurements averaging 2.7 times higher in the deblossomed trees. Similar observations were made on field-grown trees. Schaffer et al.

(1987) examined the effect of fruit removal on gas exchange of avocado leaves and observed that at 14 and 28 days after fruit removal leaf conductance was 35 to 40% lower on defruited branches than on fruiting branches. Increased leaf conductance was also observed in unthinned compared to defruited peach trees in two of five measurement periods (DeJong, 1986). In both of these two latter studies increased leaf conductance was associated with increased rates of Pn in the fruiting treatments. In strawberry both Pn and stomatal conductance were greater on fruiting plants 79 days after planting (Forney and Breen, 1985).

Reports of the effects of fruiting on leaf water potential have been variable. Jones and Cumming (1984) noted that the presence of fruit affected apple leaf water potential much less than it affected leaf conductance. Only on one of five measurement dates was there a significant fruit effect: leaf water potential was 0.07 MPa higher (more negative) than on nonfruiting branches. The researchers attributed this difference to the greater evaporation associated with the higher conductance of leaves on fruiting branches. Earlier research with apple would support the claim of a relationship between water potential and transpiration as the diurnal course of leaf water potential was the inverse of transpiration (Landsburg et al., 1975).

The daily pattern of variation of leaf water potential was not affected qualitatively by the presence of fruit in peach but the daily minimum value was lower in fruiting trees (Chalmers et al., 1983). Although this difference was again attributed to higher transpiration rates of fruiting trees, it was noted that in the early hours of the morning (when the vapor-pressure deficit was lowest) there was still a slightly lower leaf water potential in the fruiting trees. This observation was attributed to the effect of fruit growth, a separate process from the transpirational effects on leaf water potential. Increasing leaf water potentials were reported concurrently with decreasing stomatal conductance in apple (Proctor, 1981) but these observations were made late in the season and other factors (such as leaf senescence) were probably responsible.

Lakso (1979) reported a linear relationship between Pn and stomatal conductance but noted the relationship between leaf water potential and stomatal conductance changed throughout the season. Between May and September the leaf water potential required to close stomates increased by about 2.5 MPa, indicating that water potential may not be a useful indicator of Pn potential.

Girdling has been used as a research tool in growth and productivity studies with fruit trees. Heinicke (1932) reported that girdling one- or two-year-old 'McIntosh' apple trees resulted in a 42-47% reduction in Pn in leaves above the girdle six to eight days after treatment. Pn was still reduced at 30 days after treatment. He concluded that this effect was possibly a result of the harmful effects from accumulation of the products of Pn. Mika and Antoszewski (1973) reported that Pn was reduced by 50% at seven days after treatment in apple leaves as a result of bark ringing. Scoring resulted in a 21% reduction in Pn of apple leaves at 21 days after treatment but this effect was temporary and it was no longer measured at 35 days after treatment (Ferree and Hall, 1981).

Priestly (1976) used ringing to study the distribution of dry matter in young apple trees. Utilizing combinations of fruiting and defruited branches with and without ringing, he reported that apple leaves have the ability to increase dry matter production to support tree growth. Girdling has also been used to study assimilate partitioning in peach (Dann et al., 1984). Results of this latter study were similar to those of Priestly (1976) but these researchers implicated girdling effects on growth of fruit and other tree tissues was a result of altered hormone distribution within the tree rather than altered carbohydrate translocation as Priestly (1976) theorized.

Tromp and Penders (1986) used girdling to study the effects of fruiting on leaf diffusive resistance on both individual branches and whole apple trees. Leaf resistance increased within two days of treatment on ringed-defruited branches and generally continued to increase with time. Ringed-fruiting branches were not different from unringed-fruiting branches. With whole trees there was no effect until seven days after treatment. The effect of ringing on leaf resistance was attributed to the accumulation of carbohydrates (not measured) which would presumably occur more rapidly in branches than whole trees. The possible role of abscissic acid was also mentioned as a factor in the observed girdling effects on leaf resistance.

In summary, Pn is dependent upon many factors including light exposure and leaf structure. Light affects structural development of a leaf as well as its N content. Pn is positively related to leaf N content in some plant species. Carbohydrate content of a leaf also appears to affect its Pn rate with some evidence to support the feedback inhibition theory. The presence of fruit sometimes stimulates Pn, possibly as a result of carbohydrate removal from the leaf.

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Chapter I

Net Photosynthesis, Specific Leaf Weight, and Leaf Nitrogen Content of Apple Spur Leaves as Influenced by Fruiting and Light Exposure

Abstract. Net photosynthesis (Pn), specific leaf weight (SLW), and leaf N content (weight/area)(N_W) or (% dry weight)(N_P) were evaluated on spur leaves from two canopy locations of mature 'Starking Delicious' apple on four dates in 1987. Pn, SLW, and leaf N_W and N_P were all lower for interior leaves. The presence of fruit had no effect on leaf N and no consistent effect on Pn or SLW. The influence of % available photosynthetic photon flux (PPF) on the same parameters was evaluated on spur leaves of mature 'Stayman' apple throughout the growing season in 1988. A strong linear relationship existed between leaf N_W and SLW in both years. The relationships between Pn and SLW and Pn and leaf N_W were similar to each other and were also linear in both years but were not as strong. The relationship between Pn and PPF was linear on 10 June and 24 September but was quadratic for the other measurement dates while the relationship between SLW and PPF was quadratic on all dates except 24 September. The relationship between leaf N_W and PPF was considered to be linear on all dates although significant quadratic relationships did exist on some dates.

Introduction

Net photosynthesis (Pn) and specific leaf weight (SLW) of apple leaves were affected by the light environment in which a leaf developed with lower values for each parameter at lower incident light levels (Avery, 1975a; Barden, 1974, 1977; Barritt et al., 1987; Doud and Ferree, 1980; Jackson and Palmer, 1977). An average of 55% of the variation in Pn of apple leaves was explained by SLW (Barden, 1978). Based on previous studies (Barden, 1974, 1977) it was suggested that SLW could be a useful index of the previous light environment of a leaf. After a seasonal evaluation of apple leaf Pn and SLW, Porpiglia and Barden (1980) reported that both parameters were reduced with decreasing light exposure. These researchers stated that SLW may be useful in estimating cumulative light within the canopy. Marini and Barden (1981) correlated SLW with Pn throughout the season in apple and concluded that SLW appeared to be a reliable index of the previous light environment of a leaf. However, the use of SLW to predict Pn was limited to early in the season as variation in the relationship increased later in the season.

Field (1983) used a biochemically based model to predict optimal leaf nitrogen (N) distribution to maximize Pn in support of the hypothesis that leaf N was allocated for maximum efficiency of carbon gain. The model predicted that the highest N concentrations would exist in microsites receiving the highest daily light levels. Data collected from Lepechina calycina, a chaparral shrub, supported this prediction. A separate study by Field and Mooney (1983) reported similar results. A strong linear relationship between Pn and leaf N content (weight/area)

(N_w) was reported for peach (DeJong, 1982, 1983), citrus (Syvertson, 1987), and four other Prunus species (DeJong, 1983). DeJong and Doyle (1985) reported that leaf N_w was correlated with light exposure in peach canopies throughout the season. While SLW was also seasonally correlated with light exposure, the correlation coefficients were lower than those of leaf N_w. After a recent study with prune, Weinbaum et al. (1989) reported almost equal correlation coefficients for the relationships between light exposure and SLW and light exposure and leaf N_w.

Leaf N_w was higher in the upper canopy of 'Golden Delicious' than in the middle or lower canopy positions (Haynes and Goh, 1980). These differences were attributed to the effects of light exposure although actual light levels were not measured. A greater knowledge of the nature of the relationships between light exposure, Pn, SLW, and leaf N content could enable growers to provide the optimal light environment within the canopy resulting in maximum yield. The objectives of this study were: 1.) to define the seasonal relationships between PAR, leaf N content, and Pn in apple, and 2.) to compare SLW and leaf N_w as indicators of PPF in apple tree canopies.

Materials and Methods

Ten 21-year-old 'Starking Delicious'/MM.111 trees located at the Virginia Tech Horticulture farm in Blacksburg, VA were selected in 1987. The trees were spaced at 6.1 x 6.1 m and trained to a central leader. The trees were approximately 4.5 m high and had a spread of 5 m. The experimental design was a randomized complete block with the ten trees used as blocks. Fruiting (single fruit) and nonfruiting spurs were collected from heights of one to three m from both the outer and inner canopy (within one m of the trunk) on the southeast side of the trees. Spurs were collected the evening before measurement on 15 July and the morning of measurement on 6 August, 27 August, and 18 September (spurs were defruited on 11 September). Spurs were removed from the tree, recut, placed in water, and transported to the lab (Barden et al., 1974).

Pn of a single leaf/spur was measured in the lab using an Anarad model Ar-600 infrared gas analyzer in an open system. The chambers used to measure Pn were modifications of those designed by Syvertsen and Smith (1983) but without a heat exchanger. A fan in the chamber minimized boundry layer resistance. Saturating light levels of 1050 $\mu mol \cdot m^{-2} \cdot s^{-1}$ were maintained with two 500R/3FL lamps (Westinghouse). A flowing water bath between the lights and chamber removed excess heat. Air flow through the chamber was 50 $ml \cdot s^{-1}$, temperature was maintained at 28 ±1C, and relative humidity was 60% ±5%. After Pn measurement, individual leaf areas were determined using a LI-COR portable leaf area meter (Model LI-3000, Lincoln, Neb.) and leaves were oven dried for 48 hr at 65C. Leaves were subsequently ground in a Cyclone mill (UDY

Corp., Fort Collins, Col.) and % N was determined using a modified Kjeldahl technique (Bremner and Breitenbeck, 1983). The data were analyzed as a randomized complete block design using the ANOVA procedure (SAS Institute, Raleigh, NC) to test the significance of main effects and interactions. When significant interactions existed data were reanalyzed for separation of interaction means by pooling data over spur types and performing an ANOVA on girdling treatments. Data were then pooled over girdling treatments and an ANOVA was performed on spur types. For each date linear regression analyses were used to evaluate the influence of SLW on Pn and N_w and N_w on Pn.

The study was repeated in 1988 at the same location using twelve 22-year-old 'Stayman'/MM.111 trees similar in size to the trees used in 1987. Since fruiting and nonfruiting spurs did not differ in 1987, only nonfruiting spurs were used in 1988. The experimental design was a randomized complete block with the 12 trees as blocks. To yield a range of light levels, spurs were collected at distances of 0, 90, 180, and 270 cm from the trunk (± 50 cm). The height of collection was from one to three m and the dates of collection were 10 June, 24 June, 8 July, 21 July, 25 August, and 24 September. Data were collected from a single leaf/spur as described for 1987. Diffuse photosynthetic photon flux (PPF) was measured at each spur location on uniformly overcast days as close as possible to the date of spur collection (±1.5 weeks) using a LI-COR light meter (Model LI-185) and a LICOR 190S quantum sensor held horizontally at each spur position. Readings were expressed as % available PPF as measured in row middles. The data were analyzed as a randomized complete block design. Since dates differed, regression was then used to evaluate the influence of PPF on Pn, SLW, and N_w as well as the influence of SLW on Pn and N_w and the influence of N_w on Pn for each date.

Results and Discussion

The presence of fruit resulted in higher Pn than on nonfruiting spurs on 27 August but there was no effect on other dates (Table 1). There was no interaction between fruit and canopy position except on 18 September. The effect of fruit on Pn are not consistent (Flore and Lakso, 1989). Fujii and Kennedy (1985) reported average Pn rates 20 % greater in fruiting compared to nonfruiting apple spur leaves from mid-July until September. In my study there was no fruit influence on 15 July or 6 August. Ferree and Palmer (1982) reported no differences in apple spur leaf Pn in July due to the presence of fruit or fruit number (1-3). Later studies indicated no effect of fruit on apple Pn at six weeks (Rom and Ferree, 1986a) as well as 14 weeks after petal fall (Rom and Ferree, 1986a, 1986b). Rom and Ferree (1986a, 1986b) hypothesized that one possible reason for their failure to observe a fruit effect on Pn was that nonfruiting spurs used in their research were on fruiting trees and that the influence of fruiting may be general rather than localized. Studies which reported differences in Pn between fruiting and nonfruiting trees for both apple (Rom, 1987) and peach (DeJong, 1986) would support this statement by Rom and Ferree.

Fruiting spurs had lower SLW than nonfruiting spurs on 15 July but there were no differences on other dates (Table 2). Apple leaves not associated with fruit have been reported to have higher SLW (Avery, 1975b; Barritt, et al., 1987). The time of spur collection could be a factor in my observations. In this study spurs were collected the morning of measurement and nonstructural carbohydrate contents of the leaves of both types of spurs could have equilibrated during the

Table 1. Net photosynthesis (Pn) of 'Starking Delicious' apple spur leaves on four measurement dates in 1987 as affected by the presence of fruit and canopy location.

	Canopy Location		
Spur Type	Interior	Exterior	Mean
	Pn ($\mu mol CO_2 \cdot m^{-2} \cdot s^{-1}$)		
		15 July	
Fruiting	11.1[z]	17.6	14.2 a[y,x]
Nonfruiting	11.6	15.5	13.4 a
Mean	11.4 B	16.5 A	
		6 August	
Fruiting	9.0	14.0	11.5 a
Nonfruiting	10.6	13.9	12.1 a
Mean	9.8 B	13.9 A	
		27 August	
Fruiting	9.8	17.0	13.4 a
Nonfruiting	9.2	15.3	12.2 b
Mean	9.5 B	16.2 A	
		18 September	
Fruiting	9.3 aA	13.1 aA	
Nonfruiting	7.6 aB	14.7 aA	

[z] N = 10 observations per location and spur type combination.
[y] Mean separation within column (a,b) and row (A,B) by F-test, P=0.05.
[x] Main effect mean separation indicates no significant interaction.

Table 2. Specific leaf weight (SLW) of 'Starking Delicious' apple spur leaves on four measurement dates in 1987 as affected by the presence of fruit and canopy location.

	Canopy Location		
Spur Type	Interior	Exterior	Mean
	SLW ($mg \cdot cm^{-2}$)		
		15 July	
Fruiting	5.9[z]	8.3	7.1 b[y,x]
Nonfruiting	6.4	9.2	7.8 a
Mean	6.1 B	8.7 A	
		6 August	
Fruiting	6.3 aB	9.4 aA	
Nonfruiting	6.8 aB	8.7 bA	
		27 August	
Fruiting	6.3	8.8	7.6 a
Nonfruiting	6.7	9.0	7.8 a
Mean	6.5 B	8.9 A	
		18 September	
Fruiting	6.6	8.8	7.7 a
Nonfruiting	6.2	9.7	7.9 a
Mean	6.4 B	9.2 A	

[z] N = 10 observations per location and spur type combination.
[y] Mean separation within column (a,b) and row (A,B) by F-test, P=0.05.
[x] Main effect mean separation indicates no significant interaction.

previous night while still on the tree. The differences I observed on leaves collected on 15 July may reflect the fact that these spurs were collected the evening before measurement, not allowing time for this equilibration process.

SLW was lower on interior than exterior leaves for all measurement dates (Table 2) while Pn was lower on interior than exterior leaves for all dates except 18 September (Table 1). Numerous studies have indicated a positive relationship between SLW and light exposure in apple (Avery, 1975a; Barden, 1974, 1977, 1978; Barritt et al., 1987; Doud and Ferree, 1980; Jackson and Palmer, 1977). A positive relationship has been observed between Pn and SLW in apple (Barden, 1977, 1978; Marini and Barden, 1981) and peach (DeJong and Doyle, 1985; Marini and Marini, 1983).

Leaf N content, expressed as a % (N_p) or on a weight/area basis (N_w), was not affected by the presence of fruit until 18 September when it was lower on previously fruiting than nonfruiting spurs (Tables 3,4). Klein et al. (1989) reported lower leaf N_w on fruiting walnut spurs. 'McIntosh' apple trees had a higher leaf N_p when carrying a full crop than they did the following season when frost killed all the flowers (Cain and Boynton, 1948). Cropping peach trees also had higher leaf N_p than defruited trees (McClung and Lott, 1956). In this study all trees carried a normal crop so these types of comparisons cannot be made. However, I am aware of no reports in the literature comparing leaf N content of fruiting and nonfruiting apple spurs.

Table 3. Leaf N content (% dry weight)(N_p) of 'Starking Delicious' apple spur leaves on four measurement dates in 1987 as affected by the presence of fruit and canopy location.

	Canopy Location		
Spur Type	Interior	Exterior	Mean
		N_p (%)	
		15 July	
Fruiting	2.24 [z]	2.61	2.43 a[y,x]
Nonfruiting	2.19	2.57	2.38 a
Mean	2.22 B	2.59 A	
		6 August	
Fruiting	2.04	2.47	2.25 a
Nonfruiting	2.04	2.47	2.26 a
Mean	2.04 B	2.47 A	
		27 August	
Fruiting	1.99	2.38	2.19 a
Nonfruiting	1.90	2.34	2.12 a
Mean	1.95 B	2.36 A	
		18 September	
Fruiting	2.05 aA	2.23 aA	
Nonfruiting	1.86 bB	2.32 aA	

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[z] N = 10 observations per location and spur type combination.
[y] Mean separation within column (a,b) and row (A,B) by F-test, P=0.05.
[x] Main effect mean separation indicates no significant interaction.

Table 4. Leaf N content (weight/area)(N_w) of 'Starking Delicious' apple spur leaves on four measurement dates in 1987 as affected by the presence of fruit and canopy location.

	Canopy Location		
Spur Type	Interior	Exterior	Mean
	N_w ($mg \cdot cm^{-2}$)		
		15 July	
Fruiting	0.13[z]	0.21	0.17 a[y,x]
Nonfruiting	0.14	0.24	0.19 a
Mean	0.14 B	0.23 A	
		6 August	
Fruiting	0.13	0.23	0.18 a
Nonfruiting	0.14	0.22	0.18 a
Mean	0.13 B	0.22 A	
		27 August	
Fruiting	0.13	0.21	0.17 a
Nonfruiting	0.13	0.21	0.17 a
Mean	0.13 B	0.21 A	
		18 September	
Fruiting	0.14 aA	0.20 aA	
Nonfruiting	0.12 bB	0.22 aA	

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[z] N = 10 observations per location and spur type combination.
[y] Mean separation within column (a,b) and row (A,B) by F-test, P=0.05.
[x] Main effect mean separation indicates no significant interaction.

Leaf N, expressed either as a percentage or on a weight/area basis was lower on interior than exterior canopy leaves except on 18 September when there was no difference in fruiting spurs from both locations (Tables 3,4). Leaf N_p was not affected by light exposure in prune (Weinbaum et al., 1989) or walnut (Erez and Weinbaum, 1985) and altering light levels in mature 'Delicious' apple trees had no influence on leaf N content (Doud and Ferree, 1980). Jackson and Palmer (1977) reported lower leaf N_p in apple leaves the year after shading treatments had been applied than in leaves of control trees. Leaf N_p was also higher in leaves from the outer canopy of citrus than the inner canopy during the summer flush of growth (Koo and Sites, 1956) but there were no differences during the spring and fall growth flushes. I am unsure of the of the cause of the strong location effect on leaf N_p present in this study.

My observation of higher N_w in leaves of the outer than inner canopy is similar to the results from other studies. Erez and Weinbaum (1985) reported lower N_w in shaded than nonshaded walnut leaves. Leaf N_w was also observed to be highest in the upper crown position of both 'Golden Delicious' and 'Granny Smith' apple (Haynes and Goh, 1980). The differences were most pronounced in the 'Golden Delicious' trees and this effect was attributed to light exposure; the 'Golden Delicious' trees were more upright with a denser canopy than 'Granny Smith'. SLW is positively related to light exposure. Leaf N_w has been positively correlated with SLW in citrus (Syvertsen and Smith, 1984), walnut (Klein et al., 1989), and peach (DeJong and Doyle, 1985). Although my leaf N_p

was lower on interior than exterior canopy leaves, the differences in leaf N_w were enhanced by the substantial differences in SLW values for these two locations.

The interaction of spur type and location for SLW on 6 August (Table 2) reflected a greater difference in fruiting spurs between locations than in the nonfruiting spurs. I am unsure as to why this difference was present on 6 August. The interaction for leaf N_p between spur type and location on 18 September was due to the greater difference between the interior and exterior spur types as well as no difference due to prior fruiting status (Table 3). These data imply that the interior nonfruiting leaves may have been in the early stages of senescence. This would also explain the interactions for Pn (Table 1) and N_w (Table 4) also present on 18 September.

Leaf N_w accounted for 47 to 77 % of the variation in Pn while SLW accounted for 42 to 69 % in 1987 (Table 5). There was a very strong relationship between leaf N_w and SLW on all four dates.

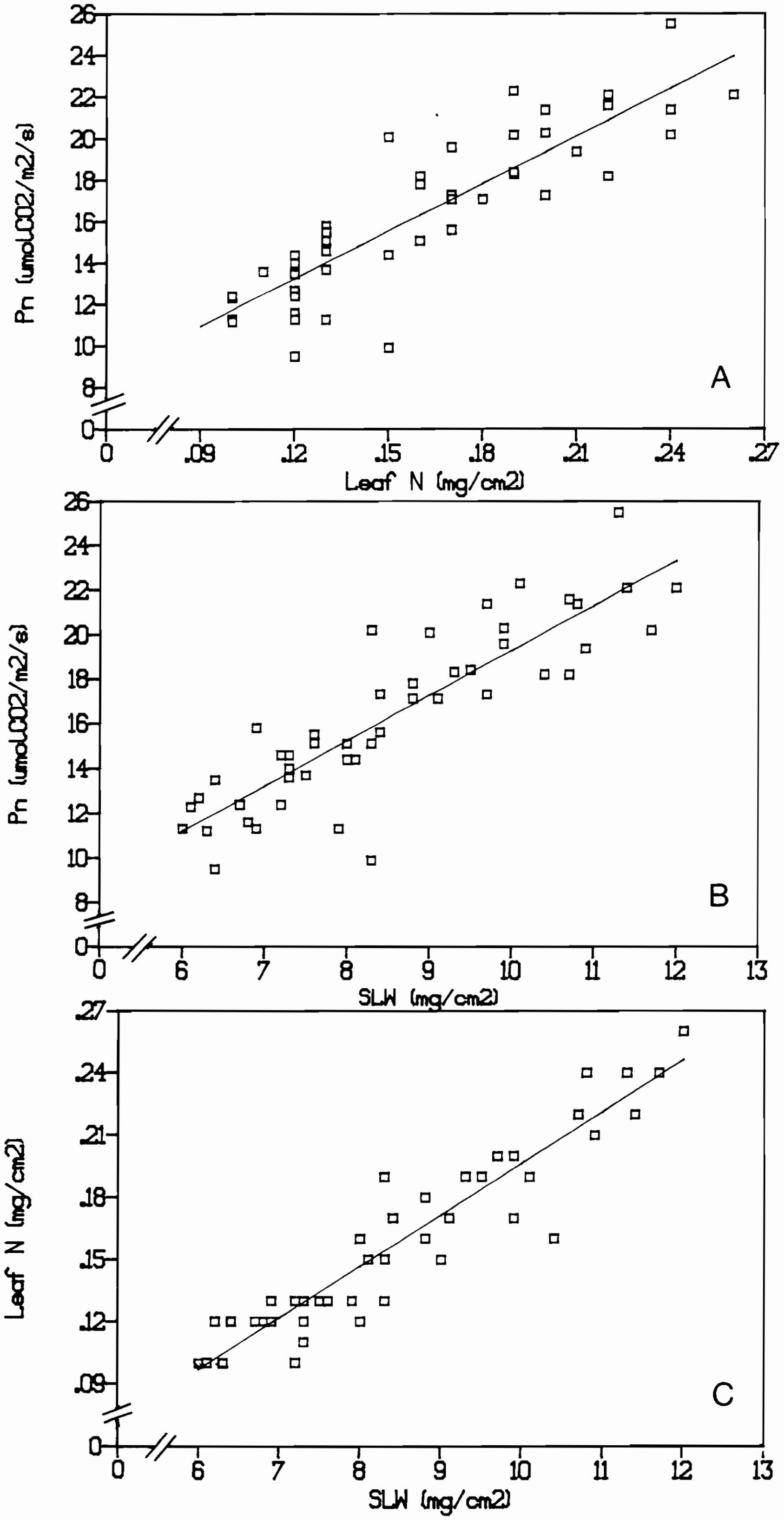
The general nature of all relationships examined in 1988 is typified by the data from 21 July. The relationships between Pn and N_w and Pn and SLW were both linear with R^2 values of 0.76 (Figure 1 A,B). The models for both relationships explained an average of 67 % of the variability in Pn for the season while the range in R^2 values for Pn and N_w was 0.62 to 0.76 and the range for Pn and SLW was 0.53 to 0.76 (data not presented). The variation in Pn explained by N_w is lower in both years than was reported in peach (DeJong, 1982; DeJong and Doyle,1985) and other Prunus species (DeJong, 1983). This could be a result of

Table 5. Regression equations and R^2 values for the relationships between net photosynthesis (Pn) and leaf N content (weight/area) (N_w), Pn and specific leaf weight (SLW), and N_w and SLW for 'Starking Delicious' apple spur leaves collected on four dates in 1987.

Relationship	Date	R^2	Equation
Pn vs N_w	15 July	0.47	$Pn = 5.69 + 45.28N_w$[z]
	6 August	0.53	$Pn = 3.85 + 44.91N_w$
	27 August	0.56	$Pn = 2.74 + 59.59N_w$
	18 September	0.77	$Pn = 1.25 + 59.01N_w$
Pn vs SLW	15 July	0.42	$Pn = 2.87 + 1.48SLW$
	6 August	0.54	$Pn = -0.23 + 1.55SLW$
	27 August	0.46	$Pn = -0.79 + 1.76SLW$
	18 September	0.69	$Pn = -1.91 + 1.67SLW$
N_w vs SLW	15 July	0.90	$N_w = -0.06 + 0.033SLW$
	6 August	0.91	$N_w = -0.08 + 0.033SLW$
	27 August	0.92	$N_w = -0.07 + 0.031SLW$
	18 September	0.87	$N_w = -0.05 + 0.028SLW$

[z] All models significant at the 5 % level, N = 40 observations per model.

Figure 1. The relationships between (A) net photosynthesis (Pn) and leaf N content (weight/area)(N_w), (B) Pn and specific leaf weight (SLW), and (C) leaf N content and SLW for spur leaves of 'Stayman' apple on July 21, 1988. The regression models are: Pn = 4.121 + 76.392N_w (R^2 = 0.76), Pn = -0.928 + 2.023SLW (R^2 = 0.76), and N_w = -0.052 + 0.025SLW (R^2 = 0.89) for A, B, and C respectively.


Pn (umolCO2/m2/s)
26
24
22
20
18
16
14
12
10
8
0
0
.09
.12
.15
.18
.21
.24
.27
Leaf N (mg/cm2)
A
Pn (umolCO2/m2/s)
26
24
22
20
18
16
14
12
10
8
0
0
6
7
8
9
10
11
12
13
SLW (mg/cm2)
B
Leaf N (mg/cm2)
.27
.24
.21
.18
.15
.12
.09
0
0
6
7
8
9
10
11
12
13
SLW (mg/cm2)
C

four factors: 1.) differences in plant species, 2.) differences in canopy densities, 3.) differences in locations of data collection, and 4.) different methodologies. The studies with peach and the other Prunus species were conducted in California where the days are predominantly clear. In Virginia many summer days are hazy or even overcast which may affect PPF at interior positions, affecting leaf physiology and thus the nature of the relationships examined. California light data were also collected over an entire day whereas my light measurements were instantaneous. Another factor could be potential differences in tree canopies. Peaches tend to form a very dense outer canopy resulting in a greater range of light values. This increased range may have resulted in a better linear relationship between Pn and leaf N_w reported in the California studies than in my study.

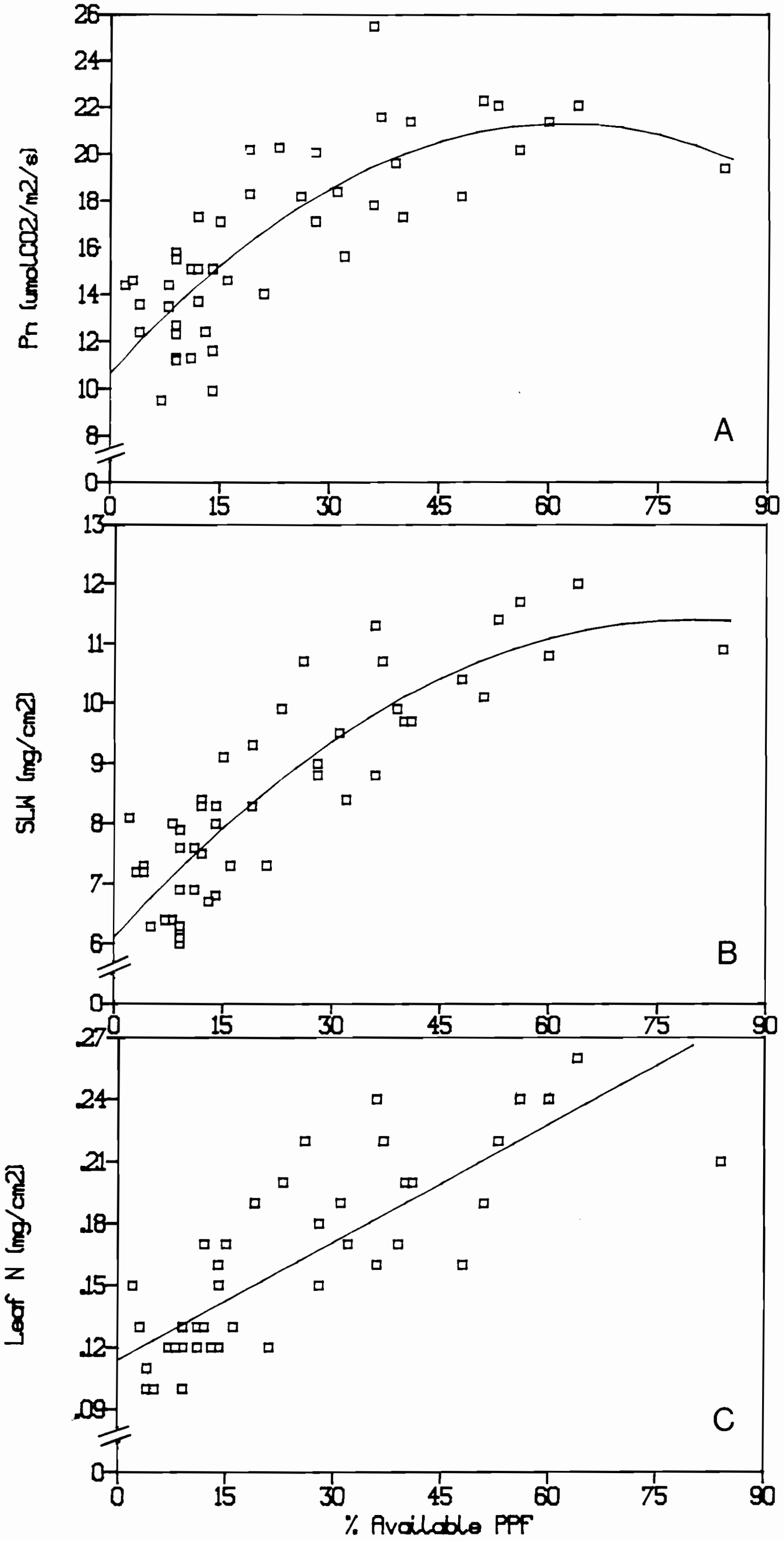
The relationships between Pn and SLW were generally stronger in 1988 than in 1987. Marini and Barden (1981) reported a linear relationship between Pn and SLW throughout the season in apple except in September when the relationship was quadratic. The R^2 values in this study are similar to those previously reported (Barden, 1978; Marini and Barden, 1981). DeJong and Doyle (1985) reported 74 % of the variation in Pn could be explained by SLW in peach. They noted that the relationships between both Pn and SLW, and Pn and N_w were very similar but that the correlation coefficient for the latter relationship was higher (r = 0.858 vs. 0.934). In my study the two relationships were essentially the same.

There was a positive linear relationship between leaf N_w and SLW on 21 July (Figure 1 C). Again this relationship was linear throughout the season and had the highest R^2 values of any relationship examined ranging from 0.85 to 0.90. The same was true for the 1987 data. The strength of this relationship implies that essentially the same information can be obtained by measuring either parameter. The ease of SLW determination would favor the use of SLW for canopy evaluation under Virginia's growing conditions.

The relationship between Pn (at light saturation) and PPF (at which the leaf developed) was quadratic (Figure 2 A). This relationship was quadratic for all dates except 10 June and 24 September (data not presented). On these two latter dates the relationship was linear but the R^2 values were below 0.50 indicating greater variability in the data. The R^2 values for the quadratic relationships ranged from 0.55 to 0.70. The relationship between SLW and PPF was also quadratic (Figure 2 B). The R^2 value was 0.76 and the R^2 values throughout the season ranged from 0.71 to 0.84. The relationship was quadratic on all dates except 24 September when it was linear ($R^2 = 0.71$).

Barden (1974, 1977) reported that the light environment an apple leaf developed in affected its Pn potential. Apple leaves from the canopy interior had lower Pn at saturating light intensities (Marini and Barden, 1981) while Porpiglia and Barden (1980) observed that leaves from the interior canopy of apple trees had lower Pn potential throughout the growing season. Lower SLW values were also observed with lower light exposure in apple tree canopies (Porpiglia and Barden, 1980).

Figure 2. The relationships between (A) net photosynthesis (Pn) (at light saturation) and % available diffuse photosynthetic photon flux (PPF) (at which the leaf developed), (B) specific leaf weight (SLW) and % available PPF, and (C) leaf N content (weight/area) (N_w) and % available PPF for spur leaves of 'Stayman' apple on July 21, 1988. The regression models are: $Pn = 10.674 + 0.346PPF - 0.003PPF^2$ ($R^2 = 0.65$), $SLW = 6.124 + 0.180PPF - 0.002PPF^2$ ($R^2 = 0.71$), and $N_w = 0.114 + 0.002PPF$ ($R^2 = 0.66$) for A, B, and C respectively.


Pn (umolCO2/m2/s)
26
24
22
20
18
16
14
12
10
8
0
A
SLW (mg/cm2)
13
12
11
10
9
8
7
6
0
B
Leaf N (mg/cm2)
.27
.24
.21
.18
.15
.12
.09
0
C
0
15
30
45
60
75
90
% Available PPF

The strength of the relationship between SLW and PPF in our study supports the use of SLW as an indicator of the light environment in an apple tree canopy (Barden, 1974, 1977, 1978; Marini and Barden, 1981; Porpiglia and Barden, 1980).

Leaf N_w was linearly related to PPF on 21 July (Figure 2 C) and all other dates (data not presented). The models explained 60 to 76 % of the variation in N_w. Significant quadratic relationships also existed on the first four measurement dates but the addition of the quadratic term accounted for only 5 % of the variation in N_w. Therefore, the simpler linear models will be discussed but the equations and R^2 values for both relationships are summarized in Table 6. DeJong and Doyle (1985) reported a linear relationship between leaf N_w and daily hours of light exposure $\geq$ 100 $\mu mol \cdot m^{-2} \cdot s^{-1}$ throughout the season in peach. In their study light exposure explained a greater amount of the variation in N_w than my data did. Again, this difference could be caused by environment, plant material, canopy structure, or methodology. Further studies are necessary to examine the causes of this difference.

Field (1983) used a biochemically-based model to predict that optimal leaf N content increases with increasing daily light exposure. DeJong and Doyle (1985) examined the relationship between leaf N content and light exposure in peach and reported that their data supported the hypothesis of a positive relationship between leaf N content and light exposure. Using unpruned trees, they observed that the slopes of the regression lines for the relationship between leaf N and daily light exposure increased throughout the season. Although the slopes of the

Table 6. Linear and quadratic regression equations with R^2 values for the relationship between leaf N content (weight/area)(N_w) and % available diffuse photosynthetic photon flux (PPF) on six measurement dates in 1988 for spur leaves of 'Stayman' apple.

Date	Linear	R^2	Quadratic	R^2
10 June	$N_w = 0.1089 + 0.00173PPF$[z]	0.60	$N_w = 0.0885 + 0.00386PPF - 0.00004PPF^2$	0.64
24 June	$N_w = 0.1161 + 0.00182PPF$	0.62	$N_w = 0.0994 + 0.00360PPF - 0.00003PPF^2$	0.67
8 July	$N_w = 0.1189 + 0.00218PPF$	0.62	$N_w = 0.0985 + 0.00449PPF - 0.00004PPF^2$	0.67
21 July	$N_w = 0.1142 + 0.00190PPF$	0.66	$N_w = 0.0976 + 0.00351PPF - 0.00002PPF^2$	0.71
28 August	$N_w = 0.1088 + 0.00197PPF$	0.76	NS	
24 September	$N_w = 0.1022 + 0.00193PPF$	0.65	NS	

[z] All models significant at the 5 % level, N = 48 observations per model.

regression lines for the relationship between leaf N content and PPF increased slightly during the season in my data (Table 6), the differences between the slopes were not statistically significant. The lack of significant slope differences in my study compared to the research on peach in California could have been caused by differing interior light levels between these two studies: the peach trees used were unpruned while my trees had been dormant pruned. Another possible factor could be the greater amount of diffuse light present under our growing conditions. This light may affect canopy interior light levels and thus the nature of the relationship.

There was a linear relationship between leaf N_p and PPF on all dates (data not presented). However, this relationship was weak (R^2 values ranged from 0.11 to 0.26) and thus N_p would not be a suitable indicator of PPF. The existence of this relationship would explain the observed differences in N_p between interior and exterior leaves in 1987 (Table 3). The low R^2 values in this relationship may also explain the inconsistency of reports in the literature as described earlier.

Pn was similarly related to both SLW and leaf N_w in both years of observation. This was probably a result of the strong relationship between leaf N_w and SLW. Pn and SLW were quadratically related to PPF most of the season in 1988 while a linear relationship existed between leaf N_w and PPF. Both SLW and leaf N_w were suitable indicators of PPF exposure. However, the ease of SLW determination would favor the use of SLW in research involving measurement of light exposure in tree canopies.

This study offered some insights into the influence of light exposure on apple leaf physiology. The results indicate that physical parameters of the leaf itself can be used to estimate light exposure within the tree canopy. Potentially, these evaluations could be used throughout the season to maintain optimal light levels within the canopy resulting in maximum yield efficiency.

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Chapter II

Apple Leaf Leaf Gas Exchange, Specific Leaf Weight, Water Potential, and Nonstructural Carbohydrate Concentrations as Influenced by Fruit and Girdling.

Abstract: The effect of fruit and girdling on net photosynthesis (Pn) and specific leaf weight (SLW) were examined on spurs of 'Redchief Delicious' and 'Stayman' apple in 1986. Pairs of fruiting and nonfruiting spurs were selected and one of each pair was girdled. At 3 days after treatment (DAT) 'Delicious' leaves on girdled-nonfruiting spurs had the lowest Pn; other treatments did not differ. Pn was similar at 7 DAT for both cultivars. At 7 DAT leaves on girdled-nonfruiting spurs had the highest SLW, girdled-fruiting spurs were the lowest, and nongirdled spurs (fruiting and nonfruiting) were intermediate. In 1988, fruiting spurs (2-3 yrs. old) on 'Red Prince Delicious' (RD) and shoots (1st year + some 2nd year wood) on 'Sundale Spur Golden Delicious' (GD) were selected with low, intermediate, and high leaf to fruit ratios; comparable nonfruiting spurs and shoots were also selected and all (fruiting and nonfruiting) were girdled. There was an interaction between spur/shoot type and time for most parameters measured on both cultivars. At 1 DAT on RD, transpiration (Tr) was higher and starch and total nonstructural carbohydrates were lower on fruiting than nonfruiting spurs. In GD the only difference at 1 DAT was lower starch concentration in the leaves of fruiting vs. nonfruiting shoots. The following effects were present in RD at 8 DAT and in GD at 4 and 8 DAT: Pn, Tr, and nonreducing sugars were greater in fruiting spurs or shoots

while leaf resistance (R_L), SLW, and starch were greater on nonfruiting spurs and shoots. Leaf water potential (ψ_L) was more negative on fruiting than nonfruiting spurs and shoots. Pn and Tr tended to decrease with time while R_L and SLW increased and ψ_L became less negative with time on nonfruiting spurs and shoots of both cultivars. Reducing sugars and sorbitol concentrations were greatest in nonfruiting spurs and shoots for both cultivars.

Introduction

The influence of fruit on apple leaf physiology is still not fully understood. The presence of fruit has been reported to stimulate net photosynthesis (Pn) in apple (Ghosh, 1973; Kazaryan et al., 1965; Monselise and Lenz, 1980b) and peach (Crews et al., 1975; Chalmers et al., 1975; DeJong, 1986). Other studies have indicated no effect of fruit on apple Pn (Ferree and Palmer, 1982; Rom and Ferree, 1986a, 1986b). Rom (1987) reported that Pn was higher on fruiting than nonfruiting apple trees at midday; earlier in the day there were no differences. Hansen (1970b) reported no difference in the uptake of $^{14}CO_2$ by fruiting vs. nonfruiting apple shoots shortly after a dark period but later in the day fruiting shoots often had 1.5 times the rate of uptake of nonfruiting shoots.

The presence of fruit can also affect specific leaf weight (SLW). Avery (1975) reported that leaves not associated with fruit had higher SLW and explained this observation as a potential accumulation of carbohydrates in these leaves. Barritt et al. (1987) made similar observations and indicated that these data support the concept of fruit as a strong sink. In a recent study to examine the effect of fruit removal on Pn and SLW of avocado leaves, it was reported that at 14 and 28 days after fruit removal SLW was 25% greater while Pn was 40-50% lower on girdled- defruited branches than on girdled-fruiting branches (Schaffer et al., 1987). At 14 days after fruit removal increased starch was observed in the leaves of defruited branches and it was concluded that this increase in starch acted as a feedback mechanism inhibiting Pn. Lower Pn as well as increased leaf starch concentrations were also reported in nonfruiting strawberry (Forney and Breen, 1985). Sorbitol, the dominant sugar in apple leaves, increased in concentration in apple leaves until mid- to late afternoon (Chong and Taper, 1971). Since apple Pn is at its maximum rate about midday and decreases throughout the afternoon (Landsburg et al., 1975), the theory of carbohydrate feedback inhibition of Pn (Daie, 1985; Gifford and Evans, 1981; Herold, 1980; Neales and Incoll, 1968) may be valid in apple.

As with Pn, the effects of fruit on other leaf physiological processes are not consistent. Fujii and Kennedy (1985) observed no differences in transpiration (Tr) or leaf resistance (R_L) between fruiting and nonfruiting apple spur leaves from May through November. In peach higher Tr was generally associated with higher Pn on fruiting trees (Chalmers et al., 1983) while in apple Monselise and Lenz (1980a) observed R_L averaging 2.7 times higher in deblossomed compared to fruiting trees. Increased leaf conductance, concurrent with increased Pn, was observed in unthinned compared to defruited peach trees on two of five measurement dates (DeJong, 1986). Jones and Cumming (1984) noted that on one of five measurement dates leaf water potential (ψ_L) was slightly more negative on fruiting than nonfruiting branches of apple. The daily pattern of variation of ψ_L was not affected qualitatively by the presence of fruit in peach but the daily minimum value was more negative in fruiting trees (Chalmers et al., 1983).

Girdling has been used as a research tool in growth and productivity studies with fruit trees. Heinicke (1932) reported that girdling 'McIntosh' apple trees reduced Pn 42-47% in leaves above the girdle six to eight days after treatment. Girdling caused an increase in leaf resistance within two days on defruited apple branches; girdled-fruiting branches were not different from ungirdled-fruiting branches (Tromp and Penders, 1986). In both of these studies the observed effects were attributed to the accumulation of photosynthates above the girdle but no carbohydrate analyses were performed. A greater understanding of the factors influencing carbohydrate production and partitioning could potentially enable growers to favor reproductive over vegetative growth, resulting in greater yields per unit land area. In my study, girdling was used to isolate spurs and shoots from the rest of the tree to observe the effects of fruit on leaf physiology. The objectives were: 1.) to examine the effect of fruit on leaf gas exchange, SLW, ψ_L, and carbohydrate content on individual spurs or shoots as affected by time after girdling and 2.) to examine the influence of varying the leaf to fruit ratio on the same parameters over time.

Materials and Methods

Twelve ten-year-old 'Redchief Delicious' apple trees, located at the Virginia Tech Horticulture farm in Blacksburg, VA, were selected in 1986 with six trees on M.9 and six on M.26 rootstocks. The trees were trained to a central leader and spacing was 1.8 x 6.1 m for M.9 and 2.4 x 6.1 m for M.26. The experimental design was a randomized complete block with the 12 trees as blocks. Pairs of fruiting (single fruit) and nonfruiting two to three-year-old spurs were selected on the south side of each tree; one of each pair was girdled by removing a 3 mm ring of bark on 10 September 1986. Pn was measured on sunny days at 3 and 7 days after treatment (DAT) as well as 8 days after harvest (15 DAT) using an ADC LCA-2 portable CO_2 analyzer (P.K. Morgan Instruments, Andover, Mass.) equipped with a Parkinson broad leaf chamber. The air flow was 6.7 $ml \cdot s^{-1}$, ambient CO_2 concentration was 345 ±15 $mg \cdot liter^{-1}$, temperature was 22 ±8C, relative humidity was 22 ±8%, and light levels were 1600 ±200 $\mu Mol \cdot m^{-2} \cdot s^{-1}$. A single leaf/spur was harvested at 7 DAT and its leaf area determined with a LI-COR portable leaf area meter (Model LI-3000, Lincoln, Neb.). Harvested leaves were then oven dried at 65C for SLW determinations. Data from this study were analyzed as a randomized complete block design by ANOVA (SAS Institute, Raleigh, N.C.). Since there was a significant spur type x treatment interaction, the data were reanalyzed by pooling over spur types and an ANOVA was performed for girdling treatments. The data were then pooled over girdling treatments and an ANOVA was performed for spur types. This experiment was repeated in the same year using eight 20-year-old 'Stayman'/MM.111 apple trees trained to a central leader and spaced at

6.1 x 6.1 m. The experimental design was a randomized complete block with the eight trees as blocks. Selected spurs were girdled on 1 October and Pn and SLW were measured at 6 DAT. The data were analyzed as described previously.

The experiment was repeated in 1988 using 12-year-old apple trees of two cultivars. The first study was conducted using four 'Red Prince Delicious' trees with one tree on M.9 (spacing 2.4 x 6.1 m), one tree on M.9/MM.111 (3.7 x 6.1), and two on M.9/MM.106 (3.7 x 6.1). The experimental design was a randomized complete block using trees as blocks. Pairs of fruiting and nonfruiting spurs with three visually-estimated leaf areas (low, intermediate, and high - mean values 45, 97, and 186 cm^2, respectively) were selected on each tree and girdled on 25 August. At 1 and 8 DAT, Pn was determined on a single leaf/spur as described previously. The leaf was then removed from the spur, the petiole was cut with a razor blade, and the leaf was placed in a pressure chamber (Scholander et al.,1965) to determine ψ_L. Tr and R_L were determined on four leaves/spur using a LI-COR Steady-State Porometer (Model LI-1600, Lincoln, Neb.). All leaves/spur were then harvested and leaf area was determined. The leaves were lyophilized, weighed, and ground in a Cyclone mill (UDY Corp., Fort Collins, Col.). Nonstructural carbohydrate components, consisting of free reducing sugars (e.g. glucose and fructose), nonreducing sugars (e.g. sucrose and fructosans), and starch were assayed using the method described by Wolf and Ellmore (1975). This procedure consists of extracting reducing sugars and hydrolyzing the nonreducing sugars and starch to reducing sugars.

These reducing sugars were then reacted with para-hydroxy benzoic acid hydrazide and the glucose concentration equivalent determined colorimetrically by measuring absorbance at 410 nm (Lever, 1972). Reducing sugars were extracted from 200 mg samples of ground leaf tissue with 20 ml of water at 100C for 45 min. A four ml aliquot was removed for assay of reducing sugars and was replaced with four ml of 1 N H_2SO_4. Nonreducing sugars were hydrolyzed during an additional 30 min. at 100C. A four ml aliquot was again removed for analysis of total sugars. Starch was extracted and hydrolyzed in the remaining 16 ml of sample by incubation in a commercial enzyme preparation (Clarase - 40,000) (Smith, 1969). After 48 hr an aliquot of the super-natant was removed and assayed. Nonreducing sugars were calculated as the difference between total sugars (acid hydrolyzed) and reducing sugars (nonhydrolyzed). Starch was calculated as the difference between total nonstructural carbohydrates and total sugar values.

Sorbitol concentrations were determined enzymatically as described by Brown et al. (1983) with some modifications. Sorbitol was extraced from a 200 mg sample of tissue in 15 ml of 80% ethanol for three hr using a microsoxhlet extractor. Alcohol was removed from the sample solution using a rotary vaccuum evaporator and the remaining extract was brought to 20 ml with distilled water. A mixed-bed resin (RG 501-X8, Bio Rad Laboratories, Richmond, CA) was used instead of Dowex 1-X8 and the concentration of NAD+ used was 13.58 mM.

The second study used six trees of 'Sundale Spur Golden Delicious'. Three trees were on MM.111 (4.9 x 6.1 m spacing), and one tree was on each of the following rootstocks: MM.106 (4.3 x 6.1), M.26 (2.4 x 6.1), and seedling (5.5 x 6.1). The experimental design was a randomized complete block using trees as blocks. Paired fruiting and nonfruiting shoots (1st year and some 2nd year wood) with three visually-estimated leaf areas (mean values 135, 273, and 420 cm^2) were selected on each tree and girdled on 8 September. Data were collected at 1, 4, and 8 DAT as described above for 'Red Prince Delicious'. Data from the two cultivars were analyzed separately as randomized complete block designs using ANOVA. Since there was usually a fruiting x time interaction, data were reanalyzed by pooling over DAT and performing an ANOVA on fruiting treatments. Data were then pooled over fruiting treatments and ANOVA was performed for each DAT. Multiple regression analyses using the MAXR procedure of SAS including first and second order terms were used evaluate the influence of reducing and nonreducing sugars, sorbitol, and starch concentrations on Pn for each cultivar. The data were first pooled and an overall analysis was performed. The data were reanalyzed by pooling over DAT and regression analysis was performed for fruiting status. The data were then pooled over fruiting status and regression analysis was performed for DAT.

Results and Discussion

There was an interaction between fruiting status and girdling treatment for both Pn and SLW on both cultivars in 1986 (Tables 1,2). Although overall Pn was higher at 3 DAT (13.13 μmol$CO_2 \cdot m^{-2} \cdot s^{-1}$) than at 7 DAT (10.53) on 'Redchief Delicious', the same treatment effects were present on both days (Table 1). There was also a main effect of treatment on Pn at 15 DAT with Pn being greater on nongirdled (12.71) than girdled spurs (3.05). Girdling had no effect on the Pn of fruiting spurs of either cultivar but reduced Pn in nonfruiting spurs. Girdling had no influence on SLW of fruiting spurs on 'Redchief' but SLW was reduced on girdled vs. nongirdled fruiting spurs of 'Stayman'. SLW was higher in girdled-nonfruiting spurs than nongirdled-nonfruiting spurs of 'Redchief Delicious' but not 'Stayman'. In girdled spurs of both cultivars fruiting spurs had lower SLW than nonfruiting spurs.

The results of this study are similar to those reported by Schaffer et al. (1987) where girdling of nonfruiting avocado branches resulted in higher SLW and lower Pn than on fruiting branches at 14 and 28 DAT. Forney and Breen (1985) also reported lower Pn and higher starch concentrations in leaves of nonfruiting strawberry plants. In my study girdling nonfruiting spurs reduced Pn at 3 DAT in 'Redchief'. Tromp and Penders (1986) reported that R_L on nonfruiting shoots increased within two days of girdling but there are no reports in the literature of this rapid an effect of girdling on Pn in apple.

There was a significant time by type interaction for most parameters measured on both cultivars in 1988 (Tables 3,4). While there are data from 1, 4, and 8 DAT in 'Sundale Spur Golden Delicious' (GD),

Table 1. Net photosynthesis (Pn) at 3 and 7 days after treatment (DAT) and specific leaf weight (SLW) at 7 DAT for 'Redchief Delicious' apple spur leaves as affected by treatment (±girdling) and spur type (±fruit) in 1986.

	Treatment	
Type	Girdled	Nongirdled
	Pn (μmolCO$_2$•m^{-2}•s^{-1})	
	3 DAT	
Fruiting	14.66 aA^{z,y}	16.35 aA
Nonfruiting	5.34 bB	16.17 aA
	7 DAT	
Fruiting	11.98 aA	13.50 aA
Nonfruiting	3.09 bB	13.55 aA
	SLW (mg•cm^{-2})	
Fruiting	10.65 bA	11.18 aA
Nonfruiting	13.04 aA	11.89 aB

[z] Mean separation within column (a,b) and row (A,B) by F-test, P=0.05.
[y] N=12 observations per treatment and type combination.

Table 2. Net photosynthesis (Pn) and specific leaf weight (SLW) of 'Stayman' apple spur leaves as affected by treatment (±girdling) and spur type (±fruit) at 7 days after treatment in 1986.

	Treatment	
Type	Girdled	Nongirdled
	Pn (μmolCO$_2$•m^{-2}•s^{-1})	
Fruiting	11.99 aA[z,y]	11.99 aA
Nonfruiting	2.43 bB	10.11 aA
	SLW (mg•cm^{-2})	
Fruiting	9.83 bA	10.60 aA
Nonfruiting	11.81 aA	10.49 aA

[z] Mean separation within column (a,b) and row (A,B) by F-test, P=0.05.
[y] N=12 observations per treatment and type combination.

Table 3. The effect of spur type (±fruit) on net photosynthesis (Pn), transpiration (Tr), diffusive resistance (R_L), leaf water potential (ψ_L), specific leaf weight (SLW), and carbohydrate concentration of spur leaves of 'Red Prince Delicious' apple on girdled spurs at 1 and 8 days after treatment (DAT) in 1988.

	DAT		DAT		
Type	1	8	1	8	Mean
	Pn (μmolCO$_2$•m^{-2}•s^{-1})		Reducing Sugars (%)		
Fruiting	8.03 aB^z	11.27 aA	3.17	3.32	3.25 b^Y
Nonfruiting	7.22 aA	1.84 bB	3.37	3.63	3.50 a
Mean			3.28 B	3.48 A	
	Tr (μgH$_2$O•cm^{-2}•s^{-1})		Nonreducing Sugars (%)		
Fruiting	3.88 aB	4.87 aA	3.66	4.51	4.11 a
Nonfruiting	3.25 bA	0.68 bB	3.38	4.75	4.06 a
Mean			3.51 B	4.63 A	
	R_L (s•cm^{-1})		Sorbitol (%)		
Fruiting	5.36 aA	2.85 bB	7.62	6.08	6.62 b
Nonfruiting	7.00 aB	28.80 aA	10.29	8.95	9.62 a
Mean			9.01 A	7.52 B	
	ψ_L (MPa)		Starch (%)		
Fruiting	-2.41 aA	-2.05 aB	2.79 bA	2.63 bA	
Nonfruiting	-2.29 aA	-1.33 bB	4.82 aB	8.21 aA	
	SLW (mg•cm^{-2})		Total Nonstructural Carbohydrates (%)		
Fruiting	11.16 aA	10.49 bB	17.26 bA	16.55 bA	
Nonfruiting	11.65 aB	12.66 aA	21.86 aB	25.54 aA	

[z] Mean separation within columns (a,b) and rows (A,B) by F-test at P=0.05. N=12 observations per type and DAT combination except Tr and R_L where N=48.

[Y] Main effect mean separation indicates no significant interaction.

Table 4. The effect of shoot type (±fruit) on net photosynthesis (Pn), transpiration (Tr), diffusive resistance (R_L), leaf water potential (ψ_L), specific leaf weight (SLW), and carbohydrate concentration of shoot leaves of 'Sundale Spur Golden Delicious' apple on girdled shoots at 1, 4, and 8 days after treatment (DAT) in 1988.

	DAT			DAT			
Type	1	4	8	1	4	8	Mean
	Pn (μmolCO$_2$•m^{-2}•s^{-1})			Reducing Sugars (%)			
Fruiting	11.54 aA[z]	13.18 aA	11.13 aA	3.40	3.15	3.42	3.32 b[y]
Nonfruiting	10.29 aA	3.81 bB	2.19 bC	3.68	3.12	3.60	3.47 a
Mean				3.54 A	3.14 B	3.51 A	
	Tr (μgH$_2$O•cm^{-2}•s^{-1})			Nonreducing Sugars (%)			
Fruiting	5.27 aC	8.96 aA	6.08 aB	6.08 aA	5.40 aAB	5.25 aB	
Nonfruiting	5.33 aA	1.89 bB	0.88 bC	6.08 aA	3.10 bC	4.07 bB	
	R_L (s•cm^{-1})			Sorbitol (%)			
Fruiting	2.12 aB	1.83 bB	2.85 bA	5.62	6.07	6.41	6.02 b
Nonfruiting	2.12 aC	15.17 aB	22.79 aA	8.15	9.27	9.35	8.92 a
Mean				6.89 B	7.67 AB	7.92 A	
	ψ_L (MPa)			Starch (%)			
Fruiting	-1.98 aA	-1.92 aA	-2.00 aA	1.77 bA	1.28 bA	2.10 bA	
Nonfruiting	-2.01 aA	-1.45 bB	-1.43 bB	2.72 aB	4.91 aA	3.13 aB	
	SLW (mg•cm^{-2})			Total Nonstructural Carbohydrates (%)			
Fruiting	11.32 aA	11.33 bA	11.68 bA	16.88	15.90	17.18	16.64 b
Nonfruiting	11.84 aB	13.32 aA	13.23 aA	20.64	20.40	20.15	20.40 a
Mean				18.76 A	18.15 A	18.71 A	

[z] Mean separation within columns (a,b) by F-test and rows (A,B) by Tukey's HSD, P=0.05. N=18 observations per type and DAT combination except Tr and R_L where N=72.

[y] Main effect mean separation indicates no significant interaction.

unfavorable weather conditions prevented an intermediate measurement on 'Red Prince Delicious' (RD).

There was no effect of leaf area to fruit ratio or leaf area of nonfruiting spurs or shoots on any of the parameters measured in this study (data not presented). Magness and Overley (1929) reported that at least 30 (and most likely 40) leaves/fruit were necessary for acceptable development of apple and pear fruit. Since this is more leaves than were present in any of the leaf-areas used in this study, the lack of a leaf-area effect could be due to all of my spurs and shoots having insufficient leaf to fruit ratios.

Pn was reduced on GD at 4 DAT on nonfruiting spurs and at 8 DAT there was a strong fruiting effect on Pn of both cultivars. In both RD and GD Pn decreased with time on nonfruiting shoots.

Tr generally followed the same trends as Pn in both cultivars (Tables 3,4). R_L varied inversely with Pn in both cultivars (Tables 3,4) - i.e. higher Pn values corresponded with lower R_L values. Apple leaf Tr followed the same diurnal pattern as Pn (Landsburg et al., 1975) and greater Pn on fruiting peach trees was generally associated with higher Tr (Chalmers et al., 1983). Schaffer et al. (1987) observed reduced Pn and Tr and increased R_L in girdled-nonfruiting avocado shoots compared to girdled fruiting shoots. Deblossomed apple trees had R_L values 2.7 times higher than unthinned trees (Monselise and Lenz, 1980a) and defruited compared to unthinned peach trees had greater R_L and reduced Pn (DeJong, 1986). Jones and Cumming (1984) also reported greater R_L on nonfruiting vs. fruiting apple trees and shoots within the same tree. Although Fujii and Kennedy (1985) did not observe any effects of fruiting on Tr and R_L, they compared fruiting and nonfruiting spurs on fruiting trees. If the effect of fruit is general rather than localized, this method may fail to detect an influence of fruiting on Tr or R_L. In the studies of Monselise and Lenz (1980a) and DeJong (1986) fruiting and nonfruiting trees were compared and in my study and the work by Schaffer et al. (1987) isolated fruiting and nonfruiting shoots were compared. This difference in methodology may be responsible for the differences between my results and those of Fujii and Kennedy (1985).

With RD ψ_L increased (became less negative) in both spur types between 1 and 8 DAT and was greater in nonfruiting than fruiting spurs at 8 DAT (Table 3). In GD there was no time effect on ψ_L in fruiting shoots while the nonfruiting shoots had greater values at 4 and 8 DAT than at 1 DAT (Table 4). Nonfruiting shoots also had lower ψ_L than fruiting shoots at 4 and 8 DAT. Jones and Cumming (1984) reported apple ψ_L was more negative on only one of five measurement periods resulting from the presence of fruit. However, from the description of their methods it is unclear whether they were comparing fruiting and nonfruiting shoots on the same tree or on different trees. Chalmers et al. (1983) observed that the daily minimum ψ_L was increased by the presence of fruit in peach. Jones and Cumming (1984) attributed the more negative ψ_L observed with fruit to higher Tr rates associated with fruiting. In my study higher Tr on fruiting shoots of GD at 4 and 8 DAT did result in more negative ψ_L than on nonfruiting shoots.

SLW in nonfruiting spurs and shoots increased as DAT increased in both cultivars (Tables 3,4). Generally, there was little change in SLW with time in fruiting spurs and shoots. As a result, SLW was higher in nonfruiting spurs and shoots than fruiting spurs and shoots at 4 and 8 DAT. The increase in SLW over time in nonfruiting spurs and shoots is similar to the data from 1986 presented in Tables 1 and 2. My data is also similar to the data presented by Schaffer et al. (1987) on avocado. In RD the TNC concentration increased in nonfruiting spurs from 1 to 8 DAT (Table 3) as did SLW of the same leaves. However, although SLW increased from 1 DAT to 4 and 8 DAT in GD, there was not a corresponding increase in TNC (Table 4). One explanation for this observation would be an increase in the structural (nonsoluble) carbohydrate components of the leaf. Although increased SLW of leaves not associated with fruit has been attributed to the buildup of carbohydrates (Avery, 1975; Barritt et al., 1987; Monselise and Lenz, 1980a), no actual measurements were made in those studies. Schaffer et al. (1987) made visual observations of increased starch grain content in cells of avocado leaves of defruited girdled shoots and concluded that a buildup of carbohydrates caused the increase in SLW of these leaves. Forney and Breen (1985) quantitatively measured increased starch in the leaves of nonfruiting strawberry plants compared to fruiting plants but no measure of TNC was made.

There were only main effects of time and type for reducing sugars for both RD (Table 3) and GD (Table 4). For both cultivars the concentration was higher in nonfruiting than fruiting spurs or shoots. In RD the concentration was greater at 8 DAT than at 1 DAT while in GD the concentration at 4 DAT was lower than at 1 or 8 DAT.

Nonreducing sugar concentrations in RD leaves were affected only by time with a higher concentration at 8 DAT than at 1 DAT (Table 3). However, there was an interaction of time and type on GD (Table 4). In fruiting shoots the concentration decreased as DAT increased. For nonfruiting shoots, the concentration also fell with time but was lowest at 4 DAT. There was no difference between types at 1 DAT but at both 4 and 8 DAT nonfruiting shoots had lower concentrations.

Sorbitol concentrations were greatest in nonfruiting spurs and shoots in both cultivars (Tables 3,4) For RD, sorbitol concentration at 8 DAT was lower than at 1 DAT. In GD, sorbitol concentration was lowest at 1 DAT, highest at 8 DAT, and intermediate at 4 DAT.

Starch concentrations were not affected by time in fruiting spurs and shoots of either cultivar (Tables 3,4). Starch concentrations generally increased with time in both cultivars on nonfruiting spurs and shoots. In GD trees, however, starch concentration was not significantly greater at 8 DAT than at 1 DAT (Table 4). Starch concentrations were consistently greater in nonfruiting spurs and shoots than in fruiting spurs and shoots on all sampling dates for both RD and GD (Tables 3,4).

Nonfruiting spurs and shoots of both cultivars had higher TNC concentrations than in fruiting spurs and shoots (Tables 3,4). In RD nonfruiting spur TNC increased from 1 to 8 DAT while TNC of fruiting spurs did not change (Table 3). TNC concentrations did not change with DAT in GD for either shoot type (Table 4).

The levels of carbohydrates reported in this study are similar to those reported previously in apple (Chong and Taper, 1971; Loescher et al., 1982). Sorbitol was the major carbohydrate present in the leaves of both fruiting and nonfruiting spurs or shoots. This is in agreement with previous reports in the literature (Chong and Taper, 1971; Hansen, 1967, 1970a; Hansen and Grauslund, 1978; Loescher et al., 1982). Sorbitol concentrations were lower in the leaves of fruiting spurs or shoots. Hansen and Grauslund (1978) reported lower sorbitol concentrations in sap of fruiting apple trees. Rom and Ferree (1986a) recently reported no differences in sorbitol concentrations of leaves on fruiting and nonfruiting apple spurs. However, the spurs were on the same tree and any "fruiting" effect was most likely present on all leaves regardless of whether or not they were adjacent to a fruit.

TNC, starch, reducing sugars, and sorbitol concentrations were all lower in fruiting than nonfruiting spurs or shoots in both cultivars. The effect on nonreducing sugars was inconsistent; in RD there was no difference between fruiting and nonfruiting spurs while in GD fruiting shoots had a higher concentration at 4 and 8 DAT.

The interrelationships between concentrations of the various carbohydrates and Pn are not totally clear; however, it is frequently proposed and there is some evidence to support the theory that sucrose and starch are critical compounds in this relationship (Champigny, 1985; Daie, 1985; Herold, 1980). Sorbitol is synthesized from the same precursors as sucrose (Marlow and Loescher, 1984); therefore, sorbitol could serve the same inhibitory role toward Pn as my data suggest.

Using multiple regression on the data from RD, 67% of the variation in Pn was explained using starch concentration (Table 5). Multiple regression analysis (by type and then by DAT) yielded models that explained from 31 to 88% of the variation in Pn and included a first or second order term for starch concentration in three of the four models (Table 5). The overall model for the data of GD explains 54% of the variation in Pn using first order terms for reducing and nonreducing sugars, starch, and sorbitol concentrations (Table 6). Two way analysis gave models that explained from 25 to 73% of the variation in Pn and included a mixture of first and second order terms (Table 6). Although significant, the models for fruiting spurs and shoots of both cultivars explained less than half of the variation in Pn than the corresponding complete model for each respective cultivar. However, the models for nonfruiting spurs and shoots of both cultivars have equivalent or greater R^2 values than their respective complete models. There is no clear trend for terms in the models when comparing the two cultivars. The concentration of starch was higher at 8 DAT on nonfruiting spurs of RD than on nonfruiting shoots on GD which may explain the more frequent occurrence of first and second order starch terms in the models in RD than in the models in GD. The differences in models between these two cultivars implies that the relationship between Pn and starch or probably any of the carbohydrates is probably not as simple as regression models would imply.

Table 5. Multiple regression models of net photosynthesis vs. various carbohydrate concentrations (first and second order terms) of leaves on fruiting and nonfruiting spurs of 'Red Prince Delicious'. (Data collected after girdling spurs on 25 August 1988).

Model	Model R^2	Terms	Prob>F
Complete[z]	0.67	Starch	0.001
Fruiting Spurs[y]	0.31	Nonreducing Sugars	0.006
Nonfruiting Spurs	0.75	Starch	0.001
1 DAT[x]	0.74	Reducing Sugars (Reducing Sugars)^2 (Starch)^2	0.009 0.001 0.001
8 DAT	0.88	Nonreducing Sugars Starch	0.007 0.001

[z] N=48 observations.
[y] N=24 observations per spur type.
[x] Days after girdling, N=24 observations per date.

Table 6. Multiple regression models of net photosynthesis vs. various carbohydrate concentrations (first and second order terms) of leaves on fruiting and nonfruiting shoots of 'Sundale Spur Golden Delicious'. (Data collected after girdling spurs on 7 September 1988).

Model	Model R^2	Terms	Prob>F
Complete[z]	0.54	Reducing Sugars	0.001
		Nonreducing Sugars	0.001
		Starch	0.008
		Sorbitol	0.007
Fruiting Spurs[y]	0.25	$(\text{Starch})^2$	0.001
Nonfruiting Spurs	0.54	$(\text{Reducing Sugars})^2$	0.007
		$(\text{Nonreducing Sugars})^2$	0.001
1 DAT[x]		NS	
4 DAT	0.73	Nonreducing Sugars	0.021
		Starch	0.001
		$(\text{Nonreducing Sugars})^2$	0.030
8 DAT	0.44	Sorbitol	0.004
		$(\text{Nonreducing Sugars})^2$	0.019

[z] N=108 observations.
[y] N=54 observations per spur type.
[x] Days after girdling, N=36 observations per date.

The presence of fruit on a girdled spur or shoot in this study enabled the leaves to maintain similar rates of Pn and Tr as well as normal R_L, ψ_L, SLW, and carbohydrate contents when examined at 1, 4, and 8 days after girdling. On spurs and shoots without fruit the ratios of carbohydrates present were altered with sorbitol and starch concentrations tending to increase with time after girdling. Gas exchange was reduced and ψ_L became less negative on nonfruiting spurs and shoots with time after girdling. Although proposed in the literature, nonstructural carbohydrate buildup in the leaves in the absence of fruit did not seem to be the only factor affecting gas exchange. There was no influence of varying the leaf to fruit ratios on any of the parameters measured on either cultivar. This observation may reflect the fact that the leaf to fruit ratio at the highest level examined was still not great enough to meet the carbohydrate requirements of the fruit. The observed response of nonfruiting spurs and shoots to girdling in this study was also independent of leaf area.

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Final Discussion

Apple spur leaves from the canopy interior had lower SLW, leaf N content (weight/area and %), and Pn at saturating light levels than leaves from the outer canopy. These effects were due to decreased light exposure as quadratic relationships were found between both Pn and PPF and SLW and PPF. There was a linear relationship between leaf N_W and PPF and although there was a significant relationship between leaf N_P and PPF, R^2 values for this relationship were below 0.30.

Research with peach in California reported that leaf N_W was a better indicator of the light environment of a leaf than SLW. In the present research SLW and leaf N_W were equivalent for estimation of light environments. Based on the results of this research, SLW would be the better indicator for assessing canopy light exposure as measurement is both rapid and less expensive than determination of leaf N_W.

Girdling reduced Pn and increased SLW on nonfruiting spurs compared to nongirdled (±fruit) and girdled fruiting spurs. At 1 DAT few differences were observed between girdled fruiting and nonfruiting spurs and shoots on two cultivars. By 8 DAT girdled nonfruiting spurs and shoots had lower Pn and Tr and greater R_L, SLW, ψ_L, and starch than fruiting spurs and shoots. Pn and Tr tended to decrease with time while R_L, ψ_L, and SLW increased with time on nonfruiting spurs and shoots. Reducing sugars, sorbitol, and TNC were greater in nonfruiting than fruiting spurs and shoots.

A buildup of carbohydrates in a leaf has been proposed to lead to reduced Pn. The results of this study are inconclusive in this area. While Pn was reduced on girdled-nonfruiting spurs and shoots of two cultivars, TNC concentration only increased in one cultivar. A greater understanding of the factors controlling photosynthate production and partitioning in apple leaves could potentially lead to the capacity to influence these processes. This could then increase yield efficiency in tree fruit crops by favoring fruiting over vegetative growth resulting in greater yield per unit land area. Other benefits from reduced vegetative growth would be reduced pruning costs and increased light penetration into the canopy interior.

Vita

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