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There has recently been a resurgence in interest in the photosynthetic efficiency of apple (*Malus domestica* Borkh.) trees. During the 1930's and early 1940's several papers were published relating to leaf morphology and the effects of various factors such as water relations, nutrition, and pesticides on net photosynthesis (Pn) of apple leaves. From the mid 1940's until the mid 1960's little relevant research was published. Renewed emphasis began to be apparent by the mid 1960's, partially as the result of greatly improved equipment, particularly the infrared gas analyzer (IRGA). This discussion is devoted to the maximum net photosynthetic potential of apple leaves, the factors which have been shown to influence it, and areas which need further research if we are to fully exploit the inherent capability for CO₂ fixation.

Maximum net photosynthetic potential

The widely varying Pn rates for apple have been recently summarized by Avery (7). Although a few researchers have reported Pn rates below 10 mgCO₂dm⁻²hr⁻¹ (34) and some above 35 mgCO₂dm⁻²hr⁻¹ (28), the great majority of reports give rates between 10 and 35. After discussing the variables which may have influenced the rates reported, Avery concluded that the maximum Pn rate of apple leaves is approx 35 mgCO₂dm⁻²hr⁻¹ (7). This is certainly well above the average Pn rate of 22 mgCO₂dm⁻²hr⁻¹ reported for apple leaves by Larcher (25). There are many factors which may result in Pn readings below the maximum of which the leaf or plant is capable. These include inadequate irradiance or air flow rates, excessive leaf temperatures, and water stress (8). Since this review relates to Pn potential, techniques affecting the Pn rates measured will not be discussed in detail as was done by Avery (7).

Among the variables which have been shown to affect the maximum Pn potential of apple leaves are cultivar (12, 13, 28, 43), rootstock (17, 43, 44), type and location of branch or spur on which the leaf is borne (9, 15, 18), light level (particularly during leaf development) (2, 9, 11), and the presence or absence of fruit or other sink (3, 4, 6, 20, 24, 34).

Cultivar

Looney reported that spur-type strains of both 'Delicious' and 'Golden Delicious' had Pn rates about 12% higher than the standard strains tested (28). Looney hypothesized that the greater Pn rates of leaves on the spur-type trees were associated with greater leaf thickness, specific leaf weight (SLW), and chlorophyll contents shown to occur in spur types by Westwood and Zielinski (45). Liu and Eaton (27) have since reported that spur type strains of 'Delicious' and 'Golden Delicious' have thicker leaves due primarily to a greater number of layers of palisade parenchyma. Looney (28) also found that both the spur and standard 'Golden Delicious' strains had higher Pn rates than either the spur or standard 'Delicious' strains tested. Ferree and Barden (17) found no difference in SLW between a spur and a standard strain of 'Delicious' nor was there a significant difference in Pn rate although the spur strain tended to have higher rates. Differences in Pn rates among cultivars have been reported by several other researchers (12, 13, 19), but it is difficult if not impossible to make direct comparisons among the experiments.

Rootstock

It is well established that apple tree productivity is dramatically influenced by rootstock. The precise ways in which the rootstock exerts its influence on the cultivar have yet to be elucidated. One research approach has been to explore the influence of the rootstock on Pn rates of scion leaves. An early report from England indicated no differences in Pn rates of leaves of a given cultivar of apple on different rootstocks (1). Since neither cultivar nor rootstocks were specified, little comparison can be made with other data. Ferree and Barden (17) reported that leaves of 2 strains of 'Delicious' had

slightly greater Pn rates when grown on MM 106 than on either seedling or M 7A rootstocks. Marro and Cereghini (33) found greater Pn rates of Richard 'Delicious' trees on M 9 than on seedling rootstocks. Using unworked rootstocks, Titova and Shishkanu (44) found that Pn rates of leaves of dwarfing rootstocks was always greater than that of leaves of seedlings. Svihra et al. (43) found that MM rootstocks produced more dry matter per unit of chlorophyll content than the M series. In 2 experiments, Barden and Ferree (unpublished) found no significant difference in Pn rates by 'Delicious' on 6 rootstocks including seedling and several clonal stocks.

In summary, the data on effects of scion cultivar and rootstock on Pn potential are inconsistent and definite conclusions cannot be drawn on the basis of published data. In general, however, it appears that differences in Pn rates due to either cultivar or rootstock are at most small and of limited commercial significance.

Leaf structure

The influence of the environment on apple leaf structure and Pn rates have been of interest for many years. In some cases there have been efforts to relate structure and Pn rates, whereas in others, only leaf structure or Pn rate has been studied. Unfortunately in many reports, it is difficult, if not impossible, to ascertain the environmental conditions with any degree of certainty. It is apparent, however, that environment during leaf development is of utmost importance in determining both leaf structure and Pn potential and perhaps the most influential parameter is photosynthetically active radiation (PAR). Unfortunately, PAR has been one of the most difficult parameters to characterize in units which are both readily measured and meaningfully related to plant response.

Early work by Auchter et al. (2) indicated that shading increased leaf size, decreased leaf thickness, and altered internal leaf structure. In a series of papers (35, 36, 37, 38, 39) Pickett presented data on internal leaf structure as well as on Pn rates as determined by diurnal changes in SLW or carbohydrate content and CO₂ uptake. Although he found differences in structure due to cultivar and rootstock, those due to environment (greenhouse vs. orchard) were greater. Because each of the 3 methods used to determine Pn rates gave somewhat different results, conclusions on the correlation between leaf structure and Pn rates were not drawn. Cowart (15) reported differences in several aspects of leaf structure associated with position on the shoot or spur.

Ghosh (18) compared internal structure and Pn rates of leaves growing on 5 to 7 year old spurs and on long terminal extension shoots. Spur leaves were thinner, had fewer layers of palisade parenchyma, shorter palisade parenchyma cells, less chlorophyll, lower Pn rates and lower SLW. The large differences reported by Ghosh would largely appear to be due to light exposure, as spur leaves were inside the canopy whereas the extension shoot leaves were on the periphery.

Leaf age

Data on seasonal trends of Pn rates by apple leaves are very limited. The general trend for other plants is an increase in Pn rate as the leaf expands, reaching a peak at about the time the leaf reaches full size (26). Seeley and Kammereck (personal communication) found that the maximum Pn rate rose rapidly during apple leaf expansion and peaked a few days after the leaf was fully expanded. These data seem to be in general agreement with the results of Slack (42) who reported that early in the life of an apple leaf, the maximum Pn rate could not occur due to immature stomates. For the earliest formed leaves, it took about 6 weeks after emergence for the stomates to mature fully. Ferree and Barden (17) reported that apple leaves showed a period of several weeks after unfolding during which Pn rates were relatively high followed by a gradual downward trend. Barden (9) more recently found that the rate of decline of Pn rate varied with light regime. Seeley and Kamereck (personal communication) found that Pn rates of apple leaves declined gradually from the time of terminal bud formation until leaf fall. Conditions such as exposure to sub-freezing temperatures drastically lower Pn potential (40). The seasonal trends in Pn potential and the many factors which may influence them warrant further investigation.

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Specific leaf weight

There have been several reports which indicate that specific leaf weight (SLW), expressed as dry weight per unit area, is dramatically affected by shade level (5, 7, 8, 9, 10, 11, 16, 23, 29). Many of these studies have involved shading of young trees growing in containers but Lakso and Carpenter (unpublished) have shown similar relationships under orchard conditions. It seems well established that as shading increases, SLW declines. Barden showed that even after leaf expansion had ceased, changed shade levels could be reflected in altered SLW (9, 11). This raises questions as to the degree to which SLW may be altered by changing shade conditions.

Skene (41) found adaptations in chloroplast structure as a result of changing shade conditions as well as during development. Shade-grown leaves had thicker grana than those grown in full sun. Shade-grown leaves transferred to sun showed no change in grana thickness but sun-grown leaves subsequently shaded showed further development and increased thickness. These data indicate that in a mature apple leaf chloroplasts can react to environmental changes, perhaps an important feature as the canopy develops.

Although the relationship between SLW and Pn rate has been implied, few data have been available. In 2 controlled shade experiments, Barden collected data on both parameters and in the more recent one has published regression lines and correlation coefficients (11). Although the slope of the regression lines varied, the trends were generally consistent. The amount of variation in Pn rate which was explained by SLW ranged from a low of 26% to a high of 82% with an average of 55%. Data from orchard conditions are presented in Fig. 1. The correlation between Pn rates and SLW was even closer than in the controlled shade studies reported previously (11).

Because SLW is so readily measured compared to Pn rate or PAR, it seems that the interrelationship between these parameters should be more fully investigated. If it is a reasonably good index of previous PAR conditions and also of Pn potential, SLW may well be useful in evaluating various orchard treatments such as pruning, tree size, and tree spacing. The use of SLW has obvious inherent advantages over previously explored indices of Pn potential such as chlorophyll content (18), internal leaf structure (15, 18, 35, 36, 37, 38, 39) and leaf thickness (15).

Presence of fruit

There have been several reports indicating that the presence of fruit leads to higher rates of Pn (3, 4, 6, 14, 21, 22, 24, 30, 31). As early as 1926, Chandler and Heinicke (14) reported that the suppression of vegetative growth brought about by fruiting was more than compensated for by the fruit produced. In a more detailed study, Maggs (30) determined the effect of cropping on the amount and distribution of the total growth increment produced. He found that cropping trees produced more total dry matter per unit area of leaf surface than did non-cropping trees. Of particular interest also was that the distribution of the growth increment into fruit was particularly at the expense of root growth. Maggs hypothesized that the assimilates produced in the leaves were diverted to the fruit rather than moving down the stem to the roots. Avery (3) reported that with 'Worcester Pearmain' on M 9, fruiting suppressed the total dry weight increment produced but that the efficiency of the foliage (calculated as g dry matter produced per dm² of leaf surface) was greater on fruiting trees. In a later study with 'Worcester Pearmain' on 4 rootstocks, Avery (4) reported that "trees of high fruitfulness produced as much, or even more, dry matter than deblossomed trees because of increased photosynthetic efficiency." However, "trees with low levels of fruitfulness produced less dry matter, including fruit, than deblossomed trees because of lower shoot growth." It appears that although the presence of fruit may increase photosynthetic efficiency per unit leaf area, the total dry weight increment produced by fruiting trees may be more or less than non-fruiting trees depending on the fruitfulness of the scion cultivar/rootstock combination.

In a series of papers, Hansen reported that the presence of fruit increased Pn rates and accelerated the translocation of photosynthates from the leaves (20, 21, 22). He concluded from several studies that the fruit acts as a strong sink and thereby causes a very efficient transfer of photosynthates from the leaves to the fruit on a given spur. A seemingly associated aspect is that Pn rates of leaves close to a fruit is higher than for leaves without a fruit in close proximity. This supports data of Kazaryan et al. (24) who found that leaves closest to fruit had the highest Pn rates.

Certain treatments to experimental plants have been shown to alter the rate of Pn or net assimilation rate (g/g/per day). Maggs (31, 32) showed that during the time of rapid growth rate, partially

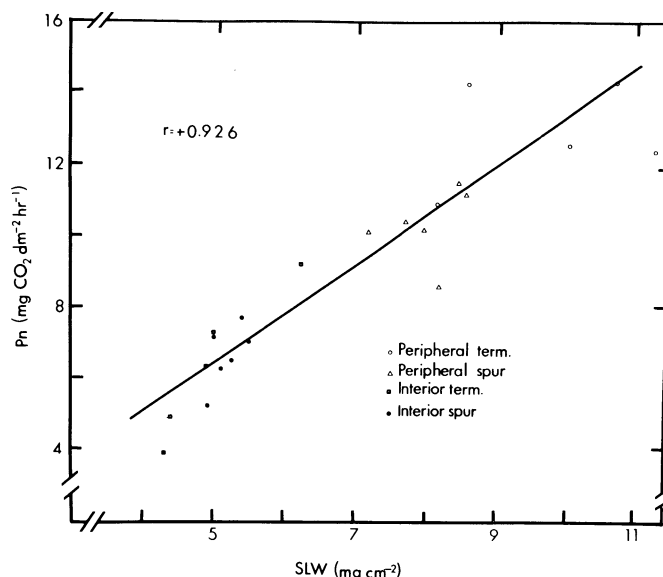


Fig. 1. The relationship between net photosynthesis (Pn) and specific leaf weight (SLW) of leaves on a 20-yr-old 'Delicious' apple tree, July 1975. Interior and peripheral spurs and terminals were detached and Pn and SLW determinations made under laboratory conditions.

defoliated trees had leaves with consistently higher net assimilation rates than comparable untreated trees. Mika and Antoszewski (34) reported that ringing and pinching of the apex or ringing alone decreased subsequent Pn rates but pinching alone had no effect. They found an accumulation of photosynthates immediately below the pinch but these materials were soon utilized by the newly activated meristem.

Although the research on the interrelationships between the photosynthetic rate of apple leaves and the presence of sinks is relatively new, this is a very productive area for further research. If we can better understand the interaction between the leaves, fruits and other sinks we may well come closer to regulating productivity.

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ENVIRONMENTALLY INDUCED RESPONSES OF APPLE TREE PHOTOSYNTHESIS¹

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Although upper limitations on photosynthesis by apple trees are imposed by the structure and biochemistry of the leaf, an apple tree has a considerable potential for the fixation of carbon. Within these limits it is important to determine factors that prevent attainment of the tree's full biological productivity. This review describes our present knowledge of some of these factors, both environmental and internal, that determine the actual biological productivity of the apple tree.

Light

Due to the variability in tree size, shape and density within an

apple planting, it is very difficult to determine the average total leaf area exposed to saturating levels of photosynthetically active radiation (PAR) at any time during the day. The fact that tree-top radiation levels fluctuate widely further complicates the prediction of the amount of leaf surface exposed to different PAR levels. Thus the prediction of the role of PAR as a limiting factor in photosynthetic reduction of carbon is a difficult task. Many of the physical parameters of apple leaves and their behavior at defined levels of radiation are well described (8, 26, 36, 40, 46, 50, 51).

The response of apple leaf net photosynthesis (P_n) to increasing irradiance is hyperbolic, a characteristic of C₃ plants (5, 6, 9, 24, 25, 36, 38, 47, 50) (Fig. 1). The photosynthetic light saturation of apple leaves has been reported to occur at 300 to 400 Wm⁻² of total solar radiation (47) or 86 to 100 Wm⁻² of incident radiation of 400 to 700 nm wavelengths (50). It is thus apparent that shading within the tree canopy, heavy cloud cover, or other conditions leading to a substantial attenuation of the solar radiation will adversely affect the net photosynthesis rate of apple leaves.

The net photosynthetic rate of an entire tree is the integral of that for all the leaves as they respond to a complex and dynamic light environment. In general, the whole tree response to increasing irradiance is hyperbolic, similar to individual leaves (24, 51). On clear

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