

NET PHOTOSYNTHESIS, SPECIFIC LEAF WEIGHT AND
GROWTH OF APPLE LEAVES AS AFFECTED BY
CANOPY POSITION AND LEAF AGE

by

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INTRODUCTION

Photosynthesis is the most vital process occurring in nature. Green plants absorb and transform radiant energy into the chemical energy necessary for the sustenance of life as we know it. The rate of photosynthesis is very dependent on the environment to which a plant is exposed and on the type of plant. Information on photosynthetic rate as affected by these factors is very useful in determining potential plant productivity.

One of the most important factors affecting photosynthesis is illumination, which varies greatly with a broad spectrum of factors. Apple trees in the orchard may have reduced illumination due to mutual shading or by shading of interior foliage by exterior foliage. The variation in illumination caused by the shading would create different environments for leaves to develop in, which could affect the photosynthetic potential of the leaves. The purpose of this study was to compare the growth, specific leaf weight (SLW), and net photosynthesis (P_n) of leaves of similar ages from the interior and exterior regions of the canopy during the growing season.

LITERATURE REVIEW

Measuring illumination in the canopy. Several devices have been used to determine illumination in apple tree canopies. Christopher (11) used a Weston illumination meter held within the north, south, east, and west sections of the tree. His data indicated a directional bias in the tree with the south receiving the maximum amount of illumination throughout the day and the north the minimum. West and east sections were similar in the amount of daily illumination measured but reached their peaks at different times during the day. Because the environment within the canopy is constantly changing throughout the day and season, many integrated readings would be more desirable than instantaneous readings. Heinicke (14) found the uranyl oxalate actinometer to be a simple, low-cost and reliable method of obtaining integrated readings on cloudless days. The actinometer consisted of a photosensitive aqueous solution of oxalic acid and uranyl sulphate contained in a test tube painted black, then white, allowing for an exposure strip completely around the tube. Placing the tubes in various portions of the tree, Heinicke (15) determined that illumination decreased rapidly as depth of foliage increased. At depths of 2.7 - 3.7 m, an average of only 25-27% full sun was measured. Heinicke reported only slight differences in illumination received among the north, south, east and west portions of the tree. He attributed differences between his and

Christopher's results (11) to the ability of the actinometer to measure sky light as well as direct sunlight, whereas the meter used by Christopher was only sensitive to direct sunlight.

Maggs and Alexander (27) investigated the validity of actinometers and noted that while they had the advantage of integrated readings, they also required positioning of the exposure strip parallel to the track of the sun as they were very sensitive to light direction. To eliminate this disadvantage, Maggs and Alexander used translucent spheres (celluloid table tennis balls) rather than test tubes. He found that the integrators could be effective in evaluating light distribution in canopies, providing exposure ceased before 70% of the uranyl oxalate was decomposed and that total irradiance was greater than $6 \mu\text{w cm}^{-2}$. Looney (24) took readings throughout trees with a spectrophotometer to measure light quality patterns on clear days. By comparing this data with that of Heinicke (15), Looney concluded that physiologically active radiation was reduced in much the same way as the radiation measured by the actinometers used by Heinicke.

Cain (9) devised his own integrating sensor for field studies which automatically accumulated the total intensity-time integral of light and temperature for days or even weeks. He found the instrument compact, portable and sufficiently economical to place a number of them in a tree for simultaneous readings. However, these instruments have not been widely tested or used by others.

A recently developed technique for describing canopies is fisheye (or hemispherical) photography. To determine the illumination reaching a given spur, Lakso (22) positioned a camera horizontally so that the fisheye lens captured the vertical hemisphere above the given spur. Pictures taken periodically during the season allowed a rapid, accurate and permanent following of illumination changes during canopy development. The pictures were then analyzed with a False Color Densitometer to determine the percentage of the image that was sky and the percentage that was canopy. Unfortunately, the Densitometer is a very expensive piece of equipment so until a less costly means of analysis is developed, this technique will be of limited use. In the same study, a Lambda quantum meter, an instrument showing much promise for light studies, was used to measure photosynthetically active radiation (PAR) reaching the given spurs. A correlation coefficient of 0.76 was found between the percent sky in the fisheye photograph and the integrated diffuse PAR.

Photosynthesis of leaves. Bohning and Burnside (7) studied apparent photosynthesis in relation to light intensity in leaves of several sun and shade species. Light saturation and compensation points for the sun species were 21.53 - 26.91 klx and 1.08 - 1.62 klx, respectively. For shade species, light saturation was reached at a maximum of 10.76 klx with the compensation point at approximately .54 klx. In a subsequent study (8), the light curves of seven "sun" species grown in deep shade were found to be very similar to those of "true" shade plants. With the exception of one species, light

saturation intensities were at least 10.76 klx lower for the shade grown plants than for similar sun grown plants. Thus, Pn of the leaves on sun plants would depend on the illumination during their growth.

Bohning (6) grew apple trees under low and high light intensities and measured their photosynthetic response under continuous illumination. Leaves developed under high intensity maintained their initial Pn rate for 18 days while leaves developed under low intensity had a rapid initial decline in Pn rate which leveled off and then remained constant for an extended time. Bohning concluded that the length of time the leaves could maintain their initial Pn rate was not only dependent on the intensity of illumination during measurement but on the previous illumination as well.

Heinicke (16) studied the effect of shade on the photosynthetic rate of apple leaves under natural orchard conditions. Using a portable infrared CO₂ analyzer, readings were taken on mid-terminal leaves that were well exposed to the sun. The same leaf was then shaded by a single leaf to obtain paired sun and shade measurements. Basic photosynthetic rates of 26.24 mgCO₂dm⁻²hr⁻¹ in sun and 7.35 mgCO₂dm⁻²hr⁻¹ in shade were determined. Heinicke proposed that by knowing the hours a certain leaf area was exposed to a particular percent of full sun and the Pn of shade and sun leaves, a daily rate of photosynthesis could be calculated.

Studying the development of tree canopy in apple hedgerows, Cain (10) observed that spur leaf development was complete by the

end of petal fall but by then new shoots were only 4 - 5 cm long with 1-2 partially expanded leaves. Spur leaves then would have developed under relatively high illumination while new shoot growth would gradually decrease the illumination available to subsequent leaves in the canopy.

Barden (4) grew young apple trees under 8 light regimes created by exposure to high or low light intensities during 3 periods of 3 weeks each. He found that Pn of leaves varied according to the light intensity during unfolding and expansion as well as subsequent light conditions.

Specific leaf weight (SLW=leaf dry wt per unit leaf area) has been investigated as an easily measured index of leaf Pn potential. Pearce et al. (30) reported that as SLW of alfalfa increased from 1.9 to 5.3 mg cm⁻², Pn increased from 20 to 50 mgCO₂dm⁻²hr⁻¹. Regression analysis indicated that variation in SLW accounted for approximately 64% of the variation in Pn. Positive and significant correlations between SLW and Pn have also been reported for apple leaves (4,5), but due to rather poor relationships from previous reports (3,13), the correlation can not be accepted as holding true under all situations. Daminozide was found to significantly increase SLW of 'York Imperial' leaves but suppressed Pn rates (13). In another study (3), Pn rates were quite comparable between 2 groups of trees in spite of large differences in SLW.

Effects of shading on growth. Shading has been shown to have various effects on the growth of apple trees. Auchter et al. (1)

covered an entire tree with a muslin tent for two growing seasons. Leaves of the shaded tree were larger and thinner than unshaded leaves and had less dry matter. Shoots of the shaded trees were longer but more slender than those on unshaded trees. Maggs (25) grew young apple trees under four levels of illumination (100%, 78%, 41% and 24% of full sun) using variously spaced lathing for shading. Contrary to the results of Auchter et al. (1), Maggs found that as the degree of shading increased, stem length decreased. Shading of the young trees also suppressed leaf number, total leaf area, leaf weight and internode length. Barden (4) reported that shading suppressed leaf number, total dry weight accumulation and shoot diameter. In a further study comparing continuous and intermittent shading of young apple trees, he found shoot length, stem dry weight and total above ground weight to be suppressed by both shade treatments while no effect was found on leaf area (5).

Effects of shading on fruit. Shading can also affect flowering, fruiting, and fruit storage qualities. Auchter et al. (1) found that artificial shading of apple trees before growth started inhibited flower bud formation, delayed spring bud opening and reduced the percent fruit set. Jackson (20) shaded trees after bloom so that pollination and fertilization would not be affected. The young fruits were shed in proportion to the severity of shading. Although the total number of fruits carried to maturity was reduced, the fruit that remained on the shaded tree were small and low in weight.

Heinicke (17) reported that both size and color of 'McIntosh' and 'Delicious' apples were correlated with the percent of full sun the fruit received. In a similar study, Jackson (18) observed that the larger and better colored apples were in the more exposed portions of the tree. In a later study, Jackson et al. (21) shaded quarters of young trees with screens made of transparent or black polyethylene slats. Shading with black slats significantly reduced the fruit diameter and fruit weight. Both shade treatments reduced fruit color considerably more than fruit size. As well as being larger and more highly colored, fruit of the outer more exposed areas were found to have different storage qualities than shaded fruit. After storage, Jackson et al. (21) found fruit of exposed areas to be more susceptible to bitter pit, rotting due to Gloeosporium spp. and soft rot than shaded fruit but less likely to develop core flush or shrivel.

MATERIALS AND METHODS

Orchard tree study. Five 20-year-old Richared 'Delicious' apple (Malus pumila mill.) trees on seedling rootstocks located at the VPI & SU Horticulture Farm orchard, Blacksburg, Va. were chosen for study. The trees, trained to a modified central leader, were 4.9 - 5.5 m in height and width and spaced so that each tree stood individually without mutual shading among trees.

On April 28, 1976, 2 weeks after full bloom, 12 shoots were tagged around the periphery of each tree at a height of about 2 m. These exterior shoots averaged 12 cm in length with 10 leaves. Twelve shoots were tagged in the interior of the tree about 2 m high and 1 m from the periphery of the tree. These interior shoots averaged 10 cm in length with 8 leaves. Shoot length and leaf number were determined at weekly intervals from April 28 to July 14. The most recently unfolded leaves were tagged at 2 week intervals (April 28, May 12, and May 26) and these leaves designated as Leaves 1, 2, and 3, respectively. Each week thereafter, length and width of the tagged leaves were measured until 2 consecutive measurements indicated that leaf expansion had ceased.

Net photosynthesis was determined for tagged leaves on an interior and exterior shoot from each tree. Just prior to sunset, an interior and exterior shoot were randomly selected from those tagged on each tree. The shoots were cut from the tree and the cut ends quickly

placed in water and recut while submerged. The shoots were taken to the lab, recut in warm water about 1.5 cm below Leaf 1 and held overnight in water-filled flasks at room conditions of 21°C and 40% relative humidity. Preliminary studies with container grown trees indicated that leaves on detached shoots had Pn rates similar to leaves on attached shoots up to 24 hrs after detachment. Net photosynthesis determinations with detached leaves have been made successfully with beans (29) and alfalfa (30). Net photosynthesis was measured by placing an attached leaf into a sealed chamber with an air flow of 3 liters per minute. Carbon dioxide concentration was measured with a Beckman Model 865 infrared analyzer and recorded on a Sargent Model SR recorder. Illumination was provided by four 500-watt Ken-Rad reflector flood lamps. A water filled plexiglas tank 18 cm deep between the lamps and leaf chamber was used to dissipate thermal radiation. Light intensity in the chamber was 39.8 klx and air temperature was maintained at 30[±] 2°C. Tests were performed on June 6, July 7, and Aug 4.

Leaf area was calculated by multiplying the product of leaf length and width by 0.71; this constant has been shown to give suitable values for apple leaves (12). Net photosynthesis was then calculated from leaf area, the change in CO₂ concentration as it passed over the leaf, and the flow rate through the leaf chamber. Net photosynthesis was expressed as mgCO₂dm⁻²hr⁻¹. Following Pn determinations, the leaf blades were removed from the shoot and

dried for 24 hrs at 80°C. Specific leaf weight was determined for each leaf by dividing dry wt by leaf area (mg cm^{-2}).

Container tree study. On May 12, 1976, 2-year-old Sturdeespur 'Delicious' trees on M 7a rootstocks were removed from cold storage where they had been stored at 2°C for the winter. The 10 trees had been grown to single stems during 1975 in 3.7 liter containers. The trees were repotted in 7.4 liter containers with a 1:1:1 (v/v/v) peat, sand, and soil mix and cut back to 3 buds.

A container tree was placed 1 m from the trunk of each of the orchard trees used in the previous experiment, and also in a full sun location on the south side of each orchard tree. These were designated as shade and sun trees, respectively. The trees were watered as required. On June 9, 1976 each tree received 0.8 g of the systemic insecticide Temik 10G (aldicarb) scratched into the soil surface. Each tree was then treated with a solution of complete fertilizer (23-19-17) at 2.6 gl^{-1} . To produce uniform plants, only 1 shoot was allowed to develop. Shoot length and leaf number were determined at weekly intervals from June 6 to August 14, 1976. The most recently unfolded leaves were tagged at 2 week intervals (June 6, June 17, June 30, July 14) and designated Leaves 1, 2, 3, and 4, respectively. Each week thereafter, length and width of the tagged leaves were determined until 2 consecutive measurements indicated that leaf expansion had ceased.

Net photosynthesis was determined on June 22, July 7, July 22, and Aug 19 for all tagged leaves. Since leaves were not detached,

Pn was determined on the same leaves on all 4 dates. The trees were taken from the orchard to the lab the evening before Pn determinations and held overnight at room conditions of 21°C and 40% relative humidity. Specific leaf weight was determined on July 22 as described previously using the next leaf to unfold after Leaf 2. On July 29, Pn was determined for Leaf 3 at intensities of 39.8, 26.9, 18.3, 12.9, 8.6, 6.5, and 4.1 klx by placing various numbers of layers of window screening between the lamps and the chambers. Light saturation of Pn was estimated from these data.

RESULTS AND DISCUSSION

The 1976 growing season was unusual in several respects. Warm temperatures in late winter brought on full bloom about 2-3 weeks early, and subsequent freezes completely destroyed the fruit crop and stunted much of the early foliage. Although there were no fruit, the spray program was adequate for insect and disease control.

Growth of orchard trees. Growth of both interior and exterior shoots ceased about June 8. Interior shoots averaged 28 cm in length with 18 leaves while exterior shoots averaged 26.7 cm with 21 leaves. Although the difference between interior and exterior shoot lengths was not significant, leaf number of exterior shoots was significantly higher than that of interior shoots. Previous studies have shown that shading suppressed leaf number and depending on the degree of shading, shoot length (5,25). However, other data shows no influence of shade on either shoot length or leaf number (4). The reasons for these variable results may relate to differences in shade level, overall vigor of the trees, and the general growing conditions.

After unfolding, Leaves 2 and 3 expanded for 3 weeks, while Leaf 1 took approximately 4 weeks to reach full expansion. These data are similar to that reported by Barden (4) for container-grown trees. About 4 leaves per shoot developed after Leaf 3, the last of which reached full expansion by mid-July. Thus, the canopy would have been fully developed by mid-July with fairly stable shade levels thereafter.

Net photosynthesis of leaves. The Pn of leaves was influenced by the canopy position. Exterior leaves had significantly higher Pn than interior leaves (Tables 1, 2 and 3). These results are similar to those of Mika and Antoszewski (28) who measured Pn of leaves growing in an interior zone of low illumination and an exterior zone of higher illumination on trees having either loose or compact crowns. The Pn of interior leaves was nearly 3 times lower than that of exterior leaves. No differences were found between the outer zone of the loose and compact crown trees but Pn in the inner zone of the loose crown tree was 4 times greater than that in the compact crown. The differences in Pn between interior and exterior leaves reported by Mika and Antoszewski are greater than those reported in the present study in which interior leaves average 60% the Pn rate of exterior leaves. Net photosynthesis was measured in the field by Mika and Antoszewski with interior leaves presumably being shaded during measurements, while exterior leaves were probably not. These readings would be more representative of actual Pn while measurements from the present study would be more indicative of Pn potential. In alfalfa, Pn of well-exposed, upper leaves has been shown to be about double that of lower, shaded leaves (32).

When leaves develop in low illumination the morphology of the leaves varies from that of sun leaves. In general, mesophyll cell size is suppressed, lamina surface is enlarged and chloroplasts may become oriented along the upper cell wall rather than the vertical walls (23).

Table 1. The influence of canopy position on net photosynthesis^z (Pn) and specific leaf weight (SLW) of 'Delicious' apple leaves at monthly intervals (Leaf 1).

Month	Canopy position		Mean
	Exterior leaves	Interior leaves	
	<u>Pn (mgCO₂ dm⁻² hr⁻¹)^y</u>		
June	14.46	9.86	12.16 a
July	13.82	9.94	11.88 a
Aug.	10.80	6.18	8.49 b
Mean	13.03 a	8.66 b	
	<u>SLW (mg cm⁻²)^x</u>		
June	8.29 a	6.49 b	
July	7.73 a	5.99 b	
Aug.	10.49 a	6.59 b	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

^xThe canopy position x month interaction was significant. Compare means within a month. Means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Table 2. The influence of canopy position on net photosynthesis^z (Pn) and specific leaf weight (SLW) of 'Delicious' apple leaves at monthly intervals (Leaf 2).

Month	Canopy position		Mean
	Exterior leaves	Interior leaves	
	<u>Pn (mgCO₂ dm⁻² hr⁻¹)^y</u>		
June	15.06	9.62	12.34 a
July	14.38	6.66	10.52 b
Aug.	11.62	5.60	8.61 c
Mean	13.69 a	7.29 b	
	<u>SLW (mg cm⁻²)^y</u>		
June	8.68	5.82	7.25 b
July	8.09	5.79	6.94 b
Aug.	10.49	6.45	8.47 a
Mean	9.08 a	6.02 b	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Table 3. The influence of canopy position on net photosynthesis^z (Pn) and specific leaf weight (SLW) of 'Delicious' apple leaves at monthly intervals (Leaf 3).

Month	Canopy position		Mean
	Exterior leaves	Interior leaves	
	<u>Pn (mgCO₂dm⁻²hr⁻¹)^y</u>		
June	8.86	6.80	7.83 a
July	12.00	6.42	9.21 a
Aug.	11.10	4.38	7.74 a
Mean	10.65	5.87	
	<u>SLW (mg cm⁻²)^y</u>		
June	7.05	5.57	6.31 b
July	8.45	5.84	7.25 b
Aug.	11.64	7.28	9.46 a
Mean	9.11 a	6.23 b	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Shade leaves are also much thinner than sun leaves (23). Presumably, many types of leaves could develop in the varied illumination within the canopy, each having a different Pn potential. This variability between leaves was overlooked by Heinicke (16) when he based the Pn rates of leaves in shaded areas on measurements from leaves that developed in sun and were then shaded for Pn determinations.

Net photosynthesis of leaves can also be affected by leaf age. The newly expanding leaf generally reaches its maximum Pn as the leaf achieves full size and then declines as the leaf ages (23). In this study, leaves in either canopy position had a downward trend in Pn as the leaf aged (Tables 1, 2 and 3). This data is similar to that of Ferree and Barden (12), where leaves of young trees reached their maximum Pn 10-40 days after unfolding and gradually declined thereafter. The trend in Pn with time varied for each leaf (Tables 1, 2 and 3). Net photosynthesis of Leaf 1 in June was similar to that in July, but declined by Aug. Leaf 2 had progressively lower Pn each month. Unlike Leaves 1 and 2, Leaf 3 showed no decline in Pn which may have been due to the differences in ages of the leaves. When Pn was determined in June, Leaves 1 and 2 were approximately at the stage of full expansion, while Leaf 3 was only 9 days past unfolding. Therefore, Leaf 3 may not have aged sufficiently during the time of study to show a decline in Pn.

Net photosynthesis would likely have been higher and the rate of decline slower if fruit had been on the trees. Leaves of fruiting trees have been shown to have greater photosynthetic efficiency than

leaves of deblossomed trees (2,26). Avery (2) calculated that leaves of fruiting trees were 21% more efficient than non-fruiting trees over the whole season.

Specific leaf weight and Pn of leaves. Interior leaf SLW averaged 69% of that for exterior leaves (Tables 1, 2 and 3). These results are consistent with those of Barden (4,5) where final SLW of leaves grown in low illumination averaged between 49 and 55% that of leaves in high illumination. Similar results have been reported with alfalfa (31,32) where high SLW was associated with high illumination.

Specific leaf weight tended to increase with age (Tables 1, 2 and 3). There was a significant interaction between time and canopy position for Leaf 1 because the difference in SLW between canopy positions in Aug was much greater than the difference in June or July. The exterior leaves did appear to increase in SLW by Aug although interior leaves remained fairly stable. For Leaves 2 and 3, SLW was similar in June and July but increased significantly by Aug.

Although apple leaf SLW increases with age at fairly constant illuminations, this pattern can be altered by changing the illumination. Barden (4) grew young trees in the greenhouse alternating 2 light levels (high and low) over 3 periods of 3 weeks each. Specific leaf weight increased from 2 to 5 weeks regardless of the light levels and continued to increase for leaves remaining in or changed to high light. Leaves continuing in or changed to low light remained relatively constant or declined in SLW.

Positive and significant correlations have been reported between SLW and Pn of alfalfa (30) and apple leaves (4,5), however, the relationship for the leaves in this study varied each month and the correlation was generally poor. In June, when the leaves were relatively young and the canopy fairly open, the r value was 0.78, a value similar to earlier studies (4,5). As the leaves aged and the canopy developed r values dropped to 0.46 and 0.40 for July and Aug. While SLW tended to increase over time, Pn decreased. Since there was neither control of shade levels nor measurements of illumination in this study, any possible relationship may have been partially masked by the various shade levels among interior leaves. These results and those of Barden (3) where leaves with very different SLW's had very similar Pn, would indicate that while SLW may be a useful index for previous illumination, it should not be considered a reliable index of Pn until more is learned about other factors affecting SLW and Pn.

Growth of container trees. Shoot growth on both sun and shade trees increased at approximately the same rate and to the final lengths of 69.1 cm and 69.0 cm respectively, with growth ceasing about July 30. Leaves reached full expansion about 3 weeks after unfolding. Leaf number was significantly higher for sun trees than shade trees, averaging 38 and 33 leaves, respectively. These data are similar to those of the orchard study and other studies (5,25). The increased leaf number of the sun trees on a similar shoot length as shade trees indicate shorter internode lengths for sun trees. These results are

contrary to those of Maggs (25) where stem length, internode length, as well as leaf number were suppressed as degree of shading increased. Perhaps shading of the container trees was not sufficient to suppress stem length. Shade trees were visibly different from sun trees. Shade trees had slender stems which required staking to remain upright and thinner leaves that were not as rigid as sun leaves. These trees could be easily separated into their respective groups upon viewing, however, orchard tree shoots could not. Since the container shade trees were placed under the orchard trees about six weeks after canopy development had started, the leaves would have developed in heavier shade than interior shoots of the orchard trees. This difference in degree of shading could account for the more noticeable differences of the container trees.

Net photosynthesis of container tree leaves. Net photosynthesis of shaded leaves averaged 63% of that for sun leaves (Tables 4, 5, 6 and 7). These results are similar to those of Barden (5) where shade leaves of greenhouse grown trees averaged about 70% that of sun leaves. Unlike the leaves of the orchard trees, the Pn rates of the container tree leaves did not decrease with time. Since these leaves started developing about 5 weeks later in the season than orchard tree leaves, the leaves may not have been old enough to show the expected decline. Also, prolonged dry periods during the summer months created a water stress condition for the orchard trees which may have affected the decline of Pn rates. This was not a problem with container trees since the trees were watered as necessary.

Table 4. The influence of full sun or shade exposure on net photosynthesis^z (Pn) of 'Delicious' apple leaves (Leaf 1).

Date	Full Sun	Shade	Mean
	<u>Pn (mgCO₂dm⁻²hr⁻¹)^y</u>		
June 22	16.88	9.84	13.36 a
July 7	8.68	11.14	9.91 a
July 22	12.30	7.56	9.93 a
Aug. 14	14.64	8.94	11.79 a
Mean	13.13 a	9.37 b	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Table 5. The influence of full sun or shade exposure on net photosynthesis^z (Pn) of 'Delicious' apple leaves (Leaf 2).

Date	Full Sun	Shade	Mean
	<u>Pn (mgCO₂dm⁻²hr⁻¹)^y</u>		
June 22	-	-	-
July 7	13.78	10.72	12.25 a
July 22	12.26	6.48	9.37 a
Aug. 14	17.84	8.66	13.25 a
Mean	14.63 a	8.62 b	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Table 6. The influence of full sun or shade exposure on net photosynthesis^z (Pn) of 'Delicious' apple leaves (Leaf 3).

	<u>Pn (mgCO₂dm⁻²hr⁻¹)^y</u>		
June 22	-	-	-
July 7	-	-	-
July 22	17.30	11.20	14.25 a
Aug. 14	17.70	9.72	13.71 a
Mean	17.50 a	10.46 a	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Table 7. The influence of full sun or shade exposure on net photosynthesis^z (Pn) of 'Delicious' apple leaves (Leaf 4).

Date	Full Sun	Shade	Mean
	<u>Pn (mgCO₂dm⁻²hr⁻¹)^y</u>		
June 22	-	-	-
July 7	-	-	-
July 22	12.44	9.76	11.10 a
Aug. 14	17.68	9.72	13.70 a
Mean	15.06 a	9.74 b	

^zPn determinations made at 39.8 klx.

^yThe canopy position x month interaction was not significant. Monthly or position means followed by a letter in common are not significantly different at the .05 level by Duncan's multiple range test.

Shade leaves were light saturated at much lower intensities than sun leaves (Figure 1). Shade leaves reached maximum Pn at about 13 klx while sun leaves had not reached maximum Pn at 27 klx. These curves are similar to those reported by Barden (5) where shade leaves were saturated at approximately 19 klx while sun leaf Pn continued to increase between 29 and 43 klx.

Specific leaf weight of leaves. Specific leaf weight of the shade leaves was significantly lower than that of sun leaves which averaged 4.51 and 8.43, respectively. Since SLW was only determined once, no aging pattern or correlation with Pn could be determined.

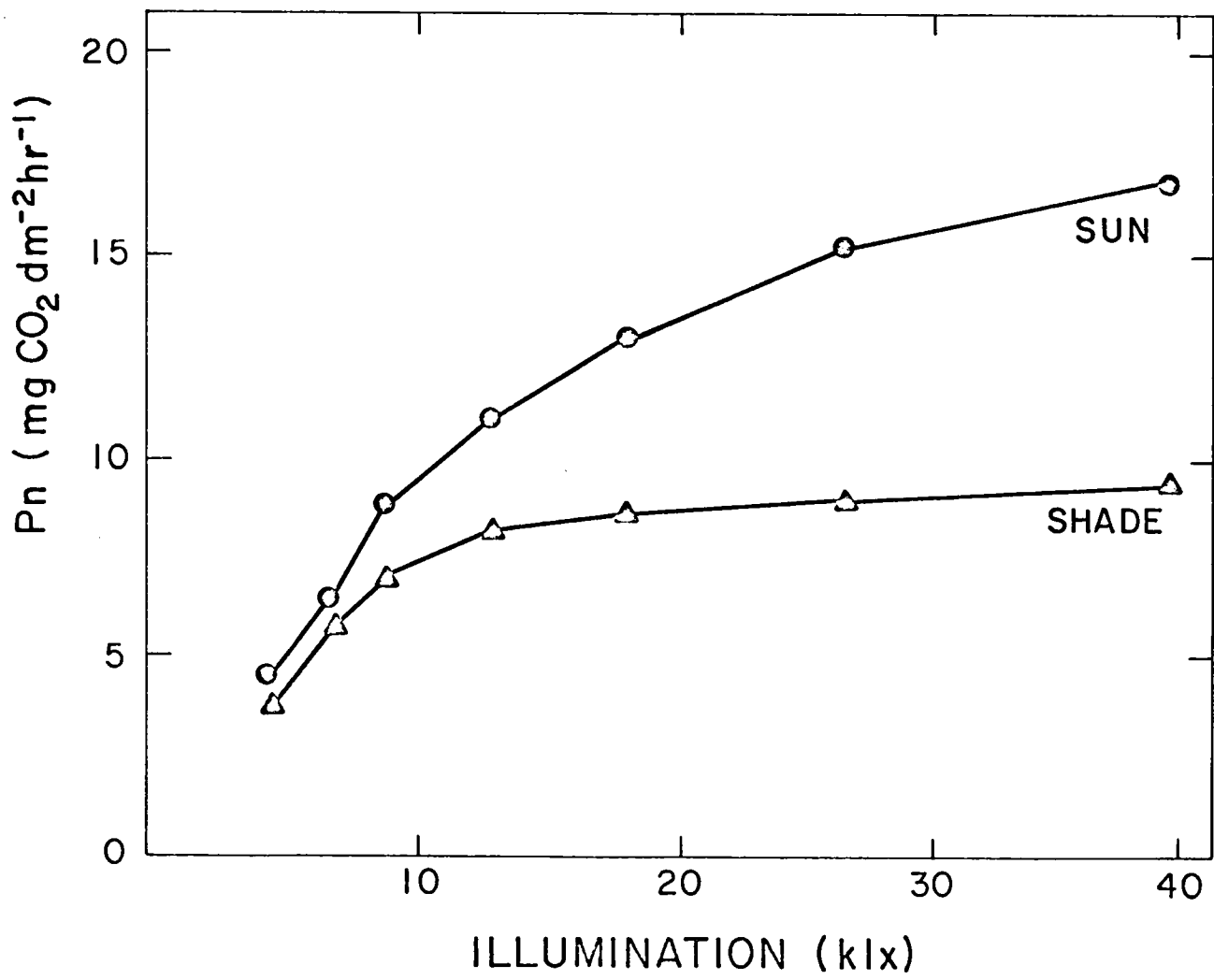


Fig. 1. Net photosynthesis (Pn) of 'Delicious' apple leaves at various illuminations as influenced by location.

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NET PHOTOSYNTHESIS, SPECIFIC LEAF WEIGHT AND
GROWTH OF APPLE LEAVES AS AFFECTED BY
CANOPY POSITION AND LEAF AGE

By

Judith Dawn Caldwell

(ABSTRACT)

Shoots were selected in both interior and exterior canopy positions on 20-year-old 'Delicious' apple trees located at the VPI & SU Horticulture Farm orchard, Blacksburg, Va. The most recently unfolded leaf was tagged on April 28, May 12, and May 26, 1976. Shoot length was unaffected by canopy position but leaf number was greater on exterior shoots. One shoot from each canopy positions was detached for determination of net photosynthesis (P_n) and specific leaf weight (SLW) of tagged leaves on June 6, July 7, and August 4. Net photosynthesis and SLW of exterior leaves were greater than that of interior leaves. As leaf age increased, P_n tended to decrease while SLW increased. No significant correlation was found between SLW and P_n . Young container trees were placed under the canopy of the orchard trees and in a full-sun location nearby. The most recently unfolded leaf was tagged on June 6, June 17, June 30, and July 14. Shoot length of the single stem tree was not affected by exposure, but leaf number was greater on sun trees. Net photosynthesis was determined on the same attached leaves at each time and was significantly higher for sun leaves than shade leaves. There were no differences in P_n as leaves aged. Specific

leaf weight was determined once and was significantly higher for sun leaves. Maximum Pn rates were reached at approximately 13 klx for shade leaves while sun leaves had not reached maximum Pn at 27 klx.