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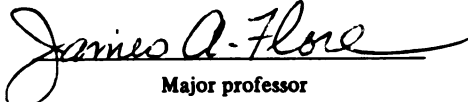
CHARACTERIZATION OF THE LIGHT MICROCLIMATE IN FOUR
PEACH TREE CANOPIES AND THE EFFECT OF SHADING ON THE
GROWTH AND LEAF PHOTOSYNTHESIS OF PEACH TREES

presented by

Frank Kappel

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By

Frank Kappel

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ABSTRACT

CHARACTERIZATION OF THE LIGHT MICROCLIMATE IN FOUR PEACH TREE CANOPIES AND THE EFFECT OF SHADING ON THE GROWTH AND LEAF PHOTOSYNTHESIS OF PEACH TREES

By

Frank Kappel

Light levels were determined at four different times during the growing season, with the use of hemispherical photography, in four peach hedgerow canopies. Greatest % sky levels occurred in the area from the top of the canopy to 25 cm below the top. On a given date there was very little difference between canopy training systems except at the 1 m level. Hedging canopies improved the light microclimate only in the top 25 cm. Spectral distribution was determined in an open center peach tree. Penetration of the various wavelengths did not parallel total radiation. Fruit maturity was directly related to % sky and negatively related to fruit number. One-year-old peach trees grown under 4 different light treatments did not differ significantly in shoot length, internode length or node number. Shade reduced average stem diameter but increased average leaf areas. Specific leaf weight and photosynthetic rate decreased as light decreased. Chlorophyll content per unit leaf area increased as light decreased but stomatal resistance was unaffected.

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LIST OF SYMBOLS AND ABBREVIATIONS

nm	nanometer
J	Joule
W	Watt
m μ	millimicron
cal	calorie
PAR	Photosynthetic Active Radiation
μ	microns
gm	gram
mg	milligram
dm	decimeter
ft.-c	foot candle
μ E	microeinstein
mcal	millicalorie

Literature Review

Tree size, spacing and training system have a dramatic effect on light conditions within the tree canopy (60, 26). Interception of light has been investigated in apples for a number of years, but very little work has been done with peaches. Commercial peach growers are increasing their planting densities, but they are limited by not having a satisfactory dwarfing rootstock. Many growers increasing their planting densities are using summer hedging to restrict the height and width of trees. A study was undertaken to determine the light microclimate in four training systems and the effect of varying light levels on growth and leaf photosynthesis of peach trees. Relevant literature concerned with light measurement techniques in fruit trees, light distribution as affected by tree architecture, and the effect of light intensity and quality on vegetative and reproductive development will be reviewed. Other effects of light such as phototropism, photoperiodism, chlorophyll synthesis and chloroplast formation will not be discussed in this review. Also, light intensity will be the only factor discussed in the photosynthesis section.

Light is an important environmental factor which influences the morphology of plants and the physiology of many plant processes. Light affects photosynthesis, chlorophyll synthesis, chloroplast formation, anthocyanin synthesis, seed germination, seedling and vegetative growth, flowering, phototropism, protoplasmic viscosity, photoperiodism and modification of biological "clocks" (3).

Gates (17) derived an energy exchange equation to describe the

energy gained and lost by a plant.

$$a_s (S + s) + a_t (R_a + R_g) = R_l \pm C + LE$$

Energy Gain

Energy Loss

where: a_s = absorptivity of the plant to sunlight

S = incident direct solar radiation and daylight

s = reflected sunlight from the ground

a_t = absorptivity of the plant to long-wave thermal radiation

R_g = incident thermal radiation from the ground

R_a = incident thermal radiation from the atmosphere

R_l = reradiation from the plant's surface

C = convection

LE = transpiration

The ($\pm$) before the C term indicates that convection will remove energy from the plant if warmer than air or transfer energy to the plant if it is cooler than air. The term light refers to the first term $a_s (S + s)$, or the global solar radiation received on a horizontal surface from the sun and sky.

Components of Light in a Fruit Orchard

Most crops are sensitive to radiation wavelengths between 400 and 700 nm (56). The basic unit of measurement for radiation is the einstein (E). Radiant flux density is the rate at which radiant energy strikes a surface of unit area. Energy units are measured in $J s^{-1} m^{-2}$ or $W m^{-2}$.

Spectral distribution of sunlight is changed because of selective spectral absorption by the leaves. Federer and Tanner (16) determined the spectral distribution of light in forests.

Reflectivity, transmissivity and absorptivity for a typical green leaf from their study is outlined in Table 1. An energy minimum occurred around 500 nm, but it was most pronounced in hardwoods on clear days. A maximum due to chlorophyll absorption occurred at 670 nm. The steep increase of energy beyond 700 nm, in the infrared is the result of decreased leaf absorption in this range. They observed that cloudy days tended to flatten out the curves, that is, make the light within the stand whiter.

The spectral patterns within apple trees on clear days is similar (41). In full shade predominant energy peaks occur at approximately 525 to 625 mμ. The estimated amount of "active" radiant energy between 400 and 750 mμ was found to decrease rapidly with increasing depth of the canopy.

Table 1. Reflectivity, transmissivity and absorptivity as a function of wavelength for a typical green leaf and for light of normal incidence in percent¹

	Wavelength* (nm)						
Measurement	400	450	500	550	670-680	740-750	1000
	%						
Reflectivity	10	8	9	21	9	49	40
Transmissivity	3	3	6	17	4	47	40
Absorptivity	87	89	85	62	87	4	20

* Interpolation between the wavelengths given is nearly linear.

¹Federer and Tanner (16).

Proctor et al. (53) found that changes in visible and infrared radiation with depth of apple tree canopy followed the same general trend as changes in total radiation. The region of greatest absorption was between 1 and 2 m from the tree top. Penetration of near-infrared (750 nm) was much greater than that of visible radiation. Penetration within the visible spectrum varied, blue (450 nm) and green (550 nm) were similar, while red (650 nm) was least and far-red (750 nm) was greatest.

Palmer (46) determined that for 'Cox's Orange Pippin' and 'Golden Delicious' leaves the mean reflectance was 7 to 9% and the mean transmittance was 1 to 4% over the visible wavelengths (400 to 700 nm) depending on leaf type. Further investigations (47) concerning the reflectance, transmittance and absorptance for sun and shade leaves of Cox's Orange Pippin and Golden Delicious, are reported in Table 2. Very small differences occurred between the sun and shade leaves.

Proctor et al. (52) found that 17% of the short-wave radiation was reflected by apple leaves and 17% was lost as long-wave radiation, leaving a net radiation of 66%. The reflection of solar radiation by an apple tree was least at solar noon and increased almost linearly with increasing solar zenith angle. All net long-wave radiation values were negative, and each day the net long-wave radiation loss rose gradually to a maximum of about $0.24 \text{ cal nm}^{-2} \text{ min}^{-1}$ at solar noon and then decreased.

Within a dwarf apple orchard light reflectance by the canopy was 19%, 53% was transmitted and 28% was absorbed by the trees (59). Of the incident PAR 7% was reflected, 42% was transmitted and 51% was

absorbed by the orchard. About 37% of the global radiation transmitted through the canopy is PAR compared with 50% of the incident radiation.

Table 2. The mean percentage leaf reflectance, transmittance and absorptance (over the 400 - 700 nm wave band) for sun and shade leaves of Cox's Orange Pippin on 1 Oct. 1973 and Golden Delicious on 27 Sept. 1973¹.

	Cox	Golden Delicious
		%
Sun leaves		
Reflectance	8.2	7.8
Transmittance	1.1	1.5
Absorptance	90.7	90.7
Shade leaves		
Reflectance	9.4	8.1
Transmittance	1.9	3.5
Absorptance	88.7	88.4

¹Palmer (46)

Instruments and Techniques for Measuring Light in Fruit Trees

A number of methods have been utilized to measure light levels in tree canopies. Light attenuation at a given leaf position is assumed to be determined by the density of foliage between that point and the sun. The foliage density varies with age and size of the tree, tree architecture (pruning) and type of tree. Light intercepted by the orchard is usually taken as the difference between the light, measured on a horizontal surface, received above the trees versus a point within the tree canopy.

Heinicke (22) used a photochemical method employing uranyl oxalate actinometers, to characterize radiation levels in apple tree canopies. A major disadvantage of this technique is that the spectral response is only from 0.222μ to 0.410μ . When data from actinometers and pyrhemometers are plotted against one another, a straight line relationship is evident on days with at least $442 \text{ gm cal cm}^{-2} \text{ day}^{-1}$; however the correlation is poor on cloudy days with less than $442 \text{ gm cal cm}^{-2} \text{ day}^{-1}$. In order for the actinometer readings to represent total solar radiation, readings are limited to cloudless days. Heinicke listed the advantages of the uranyl oxalate method for microclimate studies as: 1) simplicity; 2) low initial cost of the actinometers; 3) reliability of the readings; 4) and wide range of light conditions that can be recorded.

Cain (7) felt that photochemical methods are not adequate because of poor spectral sensitivity in the 400-700 nm range and because of their non-linearity with intensity. He therefore developed a mercury micro-coulometer for measuring light and temperature intensity-time integrals. It automatically accumulated the

total intensity-time integral for both light and temperature, for time periods of several days to weeks. However, a major disadvantage of the instrument is that neither maximum-minimum values nor the intensity at specific times are measured.

Hemispherical photography was first developed by Hill (28) in 1924 to describe cloud cover for meteorological purposes. Lakso (36) used fisheye (or hemispherical) photography to characterize light in apple tree canopies. The fisheye photograph is calibrated against the light climate at the photographic site by analyzing the percentages of the hemispherical photograph occupied by sky versus canopy. The assumption before calibration is that the percentage of the photograph that is sky is proportional to the light reaching the site. Lakso (38) reported good correlations of the % sky with total and diffuse light, sunfleck penetration, red/far-red ratios, flowering and fruit colouration. A number of methods exist for photograph analysis, including the overlay grid method, measurement of transmission of the transparency, and the use of a false colour densitometer. There are some disadvantages with the fisheye technique: canopy gaps near the horizon give disproportionate % sky values while representing sky of lower than average luminosity, and exact calibration of the fisheye analysis is difficult.

Pyranometers uniformly sensitive to all wavelengths from 300 to 3500 nm were used by Proctor et al. (53) to obtain measurements of global radiation within an apple tree canopy. Photosynthetically active radiation (PAR) can be measured with a quantum sensor meter (400-700 nm sensitivity) (37, 33).

The Effect of Light Intensity and Quality on Vegetative and Reproductive Development

A discussion of the radiation microclimate of fruit trees would not be complete without considering the effects of light level and light quality on photosynthesis, overall growth (vegetative), flowering, and fruit set and development. Again, much of the work has been done with apple trees.

Photosynthesis. Sestak et al. (57) reports that there are 9 possible ways of measuring photosynthesis, including measuring: a) the change in energy; b) the composition of water; c) oxygen efflux; d) influx of carbon dioxide; e) dry matter accumulation; f) accumulation products; g) accumulation of energy; h) rate of formation of energy rich intermediates, and i) properties of the photochemical apparatus. The measurements of a) and b) are very difficult to determine and are rarely used. The gasometric methods (c) and (d) those most commonly employed with (d) being used most often with higher plants. Simultaneous measurements on a large amount of tissue or number of treatments are possible with methods mentioned in (e) to (g). Methods (h) and (i) require complicated apparatus and isolated chloroplasts or pretreated plant material.

Heinicke (26) reported two basic Net Assimilation Rates in apple trees. The rate in direct sun ($26.24 \text{ mgCO}_2\text{dm}^{-2} \text{ hr}^{-1}$) was more than 3 times greater than that in shade ($7.35 \text{ mgCO}_2\text{dm}^{-2} \text{ hr}^{-1}$). He reported that there are essentially two photosynthetic zones in apple trees which correspond to light intensity. The compensation point, that light intensity at which respiration and assimilation are equal appears to be very low in apple leaves since it was not reached,

except in a few instances, even at the low light intensities. It probably rarely occurs during the day under natural conditions in apple trees of the type studied here. Proctor et al. (54) estimated the compensation point to be about 12 Wm^{-2} .

Mika and Antoszewski (44) confirmed Heinicke's work by using a ^{14}C technique to determine gross photosynthesis. The photosynthetic efficiency of leaves in the outer zone of the tree crown was about 3 times greater than that of leaves in the inner zone, and the maximum rate of photosynthesis on a hot day occurred between 8:00 and 10:00 a.m. before irradiance had reached its maximum.

The leaves of long apple shoots exhibit higher photosynthetic rates than those of spurs (20). The presence of fruit on the shoots also influences photosynthetic activity, leaves of fruit-bearing shoots having higher photosynthetic rates than those of shoots without fruit.

Spur type mutants of 'Delicious' and 'Golden Delicious' apples averaged approximately 12% higher Net Assimilation Rates than those of the parent cultivars (42).

Vegetative Growth. Barden (2) found no effect of light treatments on apple shoot length, leaf number or total leaf area. The apple trees were exposed to combinations of 2 light levels in 3 periods. High light was full greenhouse sun and low light was 20% full sun. Leaf thickness was greater under higher light intensities due largely, but not entirely, to the increased thickness of the palisade layer. The individual palisade cells were longer in such "sun leaves" and the numbers of layers of palisade cells tended to be greater.

Flowering. Cain (8) found that virtually no apple flowers were initiated at light values less than about 30% of available light and there was essentially no difference in flowering above the 70% light level. Later (9) he noted that within certain lower limits, the formation of flower buds was directly related to spur leaf area and light exposure. Each spur was independent of other leaves on the tree for flower initiation. Defoliating individual spurs, or one portion of branched spurs resulted in failure to produce flowers with no effect on adjacent spurs. The most critical time for illumination of spur leaves is prior to mid-July when flower buds usually have been initiated.

Lavee and Erez (39) determined that opening of peach leaf buds on excised shoots required light, and the active range for the process was 600-690 nm. However, opening of flower buds was relatively light independent.

Fruit Characteristics. 'Red Delicious' fruit which received more than 50% FS was larger than more heavily shaded fruit (27). Fruit exposed to more than 70% FS exhibited best colour and sufficient colour for the Extra Fancy Grade did not develop on fruit exposed to less than 50% FS. Heinicke (27) described 3 distinct light zones in apple trees which affect quality: 1) inadequate light for production of marketable fruit with less than 40% FS; 2) an adequate light zone with from 40-60% FS and; 3) a light zone above 60% FS for the optimum development of fruit quality.

Cain (9) determined that apple fruit development and rate of maturation are generally related to the mean leaf area per fruit for the entire tree. Heavy shading reduces fruit diameter, fruit weight

and red colour development in apple (29). The poor light conditions in the interior and basal parts of apple hedgerows are reflected in low values for fruit weight and especially colour (59).

Apple colour is positively correlated with global radiation reaching the fruit (53). Proctor and Creasy (51) observed that a minimum of $10 \text{ cal cm}^{-2} \text{ day}^{-1}$ was necessary for the initiation of anthocyanin synthesis in 'McIntosh' apple, but that more than $250 \text{ cal cm}^{-2} \text{ day}^{-1}$ was required to obtain a large percentage of highly coloured fruit.

In England (14) shading raised the concentration of calcium and potassium in apple fruit and lowered those of dry matter and starch. The authors suggested that shading delays the time of maximum fruit maturity.

Light Distribution in Fruit Tree Canopies

Proctor et al. (53) found 3 zones of global radiation absorption within an apple tree canopy. Little absorption occurred on the periphery; a zone of strong absorption occurred between 1 and 2 m from the tree top; with a zone of moderate absorption at 2 to 2.6 m.

Heinicke (26) determined that on clear, bright days there were only 2 light zones in apple trees, a high light intensity zone of between 6000 and 11,000 ft.-c., in direct sun and low intensity zone of 400-700 ft.-c., in shade. Shade from a single leaf reduced light intensity by this amount while additional shading did not reduce light intensity.

In citrus trees less than 1% of the total net radiation above the canopy penetrated to a depth of 4 ft. from the ground while some

90% was absorbed in the upper 3 ft. of the canopy (21). Of this, 44% was absorbed in the first foot of the canopy on the cloudy-bright day, and 67% on the cloudy day. Thus radiation penetrated to a greater depth into the canopy of the large tree on the cloudy-bright day. Comparisons were made between large (25 ft.), medium (18 ft.) and small (8 ft.) orange trees and it was found that radiation penetrated deeper into the medium and small tree than into the large tree.

Leaf Area Indices (LAI) have been compared with light levels. Llevelyn (40) postulated that LAI along the lines of the sun's rays would be a better estimate of light attenuation within the tree canopies than LAI above the measuring point and developed a computer program to calculate these LAI. Although the resultant output consisted of a plan of the foliage density as seen from the position of the sun, the data did not correlate well with light attenuation.

Heinicke (23) also found quite a reduction in foliage distribution and light levels towards the lower and center portions of the tree. However, greatest reduction was not in the center, but at a point between the edge and tree center. Average light density was reduced from 93% FS on the top level to 70% FS 3 ft. down, 42% FS at 6 ft., 25% at 9 ft. and 21% FS at 12 ft. The foliage was quite evenly distributed from the top to the bottom of the trees and in the N, S, E and W sides of the trees. He concluded that a LAI of ca. 4 to 5 is about the maximum which will allow sufficient light (for the maximum photosynthetic rate) to strike all foliage. For this assumption a figure of 25% to 30% FS is considered to be the adequate minimum.

The PAR available to a shaded site within an apple tree canopy is dependent not only on the density of the canopy to light penetration, but also on the amount of diffuse light available to the tree. Lakso and Musselman (37) compared light levels in apple tree canopies on clear bright days, dull overcast days, and partly cloudy days. The interior light levels on dull (exterior PAR = $1100 \mu\text{Em}^{-2} \text{s}^{-1}$) days were about 3 times that on either the clear or overcast days. Interior light was greatest when the total light was between 60% and 90% of the maximum for clear sky conditions. This occurred when cloud cover was light enough to transmit and reflect high amounts of radiation, giving higher levels of diffuse light.

A single apple leaf effectively blocks out direct light, leaving only diffuse light in the shaded area (24). On days with heavy cloud cover, when the position of the sun is obscured, there is little difference between total and diffuse light, and shading has less effect on light intensity than clear days. Cloud cover reduces the total radiation, however diffuse light is greater than on a clear day, which results in more light on cloudy than bright days in shaded portions of the tree.

Light measurements before and after fruit removal suggest that the shade cast by the fruit is negligible as compared to shading by the foliage (60). However, for a large apple tree the average light intensity under the leafless canopy in winter was only 67% of full sun, indicating considerable shading by limbs alone (30).

As tree size increases the canopy area with less than 30% FS also increases (25). As a result more foliage per acre is favourably exposed to light than in semi-dwarf or standard trees.

Verheij and Verwer (60) compared apple trees on M9 (dwarfing) versus M2 (semi-standard) rootstocks. Light levels in the lower interior of the tree were 15% and 10% of full light in the M9 and M2 hedges, respectively.

Jackson (30) compared light intensities in "bush" trees. The bush trees (4m high) were maintained as individuals but some touched or overlapped with neighbouring trees in the rows, while in hedge trees (2-2.5 m high) the branches of adjacent trees were allowed to intermingle in the row. In the main cropping zone of bush trees light intensity ranged from 35% to 95% of full sun; while light intensity deep in the center averaged 17% of full sun. Light intensity at the center of a 2 m hedge averaged between 5% to 11% of full sun, while in the main cropping zone near the surface of the hedge it averaged between 10% to 95% of full sun. Reduction in light intensity within a row caused by lateral shading was estimated by measuring the light intensity at different heights in the center of a double-width alley, i.e. where a hedgerow was omitted. Light intensity was reduced to 67%, 80%, and 95% at 0.5, 1.0 and 1.5 m above ground, respectively.

When comparing hedgerow to bush trees, Mika and Antoszewski (45) found that trees grown in hedgerow systems have higher light interception values than trees trained as bushes. They concluded that over 80% of available light is intercepted when the hedgerow height is equal to the alleyway width, and $\frac{1}{2}$ of the ground area is covered by hedgerows.

Row orientation has a profound influence on light penetration and interception in apple orchards. Devyatov and Gorny (13) found

that interception of PAR interception on the eastern wall of North-South oriented rows equalled about $220 \text{ mcal cm}^{-2} \text{ min}^{-1}$ in the morning; in the afternoon it decreased to 60 and in the evening to 25 mcal. Radiation on the western wall increased over the same period. The tops of the trees at a height of 3 m received equal amounts of PAR in N-S and E-W rows. Downward in the crowns the intensity of sun radiation decreased, but in a different way; at a height of 2 m intensity was 70-75% in N-S rows, and 85% in E-W ones. At a height of 1 m it was 30-35 and 60-65% respectively. They concluded that E-W row orientation of the espalier apple orchard increased the interception of PAR by 15-26% and yield by 16-35%.

SECTION I

SEASONAL CHARACTERIZATION OF THE LIGHT MICROCLIMATE IN
FOUR PEACH (PRUNUS PERSICA (L.) BATSCH.) HEDGEROW CANOPIES

Abstract. Light levels were determined by hemispherical photography at 4 different times during the growing season, in 4 peach hedgerow canopies: oblique fan, canted oblique fan, modified central leader and open center. Greatest % sky levels occurred in the area from the top to 25 cm below the top of the canopy. Canted oblique fan had the highest % sky value (98%) on July 18 while the lowest reading (26%) occurred in oblique fan August 21. There was very little difference between canopy training systems except 1 m above the ground. Hedging improved the light microclimate in the canopies only within the top 25 cm. Spectral distribution determined in an open center tree did not follow the general trend of total radiation. As shading increased, not all wavelengths were absorbed equally, resulting in a decrease of the visible to infrared ratio. Fruit maturity was directly related to % sky and negatively related to fruit number. Percent sky and fruit number combined, accounted for 40.7% of the variation in fruit maturity.

Solar radiation influences a number of plant morphogenic and re-productive responses which affect fruit productivity. Shading reduces flower bud development and fruit size, quality and colour (8, 9, 27, 29, 53, 60).

Several studies have characterized light regimes in apple trees. Proctor et al. (53) found that little absorption occurred on the periphery; a zone of strong absorption occurred between 1 m and 2 m from the tree top, and a zone of moderate absorption at 2 m to 2.6 m. Jackson (3) reported that the light intensity deep in the center (1 m from the ground) of a "bush" tree averaged 17% of full sun while in hedge trees light intensity at the center of a 2 m hedge averaged between 5% to 11% of full sun between 1 m and 0.5 m from the ground. Trees grown in hedgerow systems generally intercept light to a greater degree than "bush" trees, and therefore utilize available light more efficiently than "bush" trees (45).

Tree size has a profound influence on the volume of the tree that is shaded. Heinicke (25) determined that percentage of the leaf area which receive insufficient light, less than 30% full sun, decreases as tree size decreases.

Interception of light has been investigated in apples for a number of years, but very little work has been done with peaches. Yield increases with planting density (15, 49); although commercial growers are increasing their planting densities, they are limited by not having a satisfactory dwarfing rootstock. With judicious use of pruning and summer tipping to train and restrict growth, tree walls can be formed to permit efficient management of the orchard. Data are needed on light distribution in high density tree wall plantings

so that the most ideal orchard design and training system can be utilized.

The objectives of this study were: a) to characterize the light microclimate in the bearing surface in four training systems (oblique fan, canted oblique fan, modified central leader and open center trees); b) to determine the spectral distribution of solar radiation within the canopy of an open center tree; and c) to determine the effect of light intensity on fruit maturity.

Materials and Methods

Peach (Prunus persica (L.) Batsch) trees were planted in 1969 in four hedgerow systems: a) oblique fan (OF); b) canted oblique fan (COF); c) modified central leader (MCL); and d) open center (OC). Each training system was represented by a single row of trees oriented north to south with respective in row spacing of a) 4.9; b) 2.4; c) 3.0; and d) 4.3 m and row spacing of 3.6 between OF and COF, 5.5 m between COF and MCL and 6.1 m between MCL and OC (19). From 1974 to 1979 tree walls were maintained to a uniform height of 3 m and tree wall widths of a) 1.5; b) 2.0; c) 3.0; and d) 3.0 m, respectively, by mechanical hedging using a Durand Wayland Tree Topper and Hedger in mid-July. In 1979 dormant pruning consisted of removing only the dead wood and trees were summer hedged July 12. Vegetative growth was permitted to fill the available space within the row.

Three trees in each treatment were selected in 1978 and three different trees in 1979. Nine positions were used in 1978 and 15 in 1979 in each tree as illustrated in Figure 1.

Fisheye, or hemispherical, photography was used to estimate the

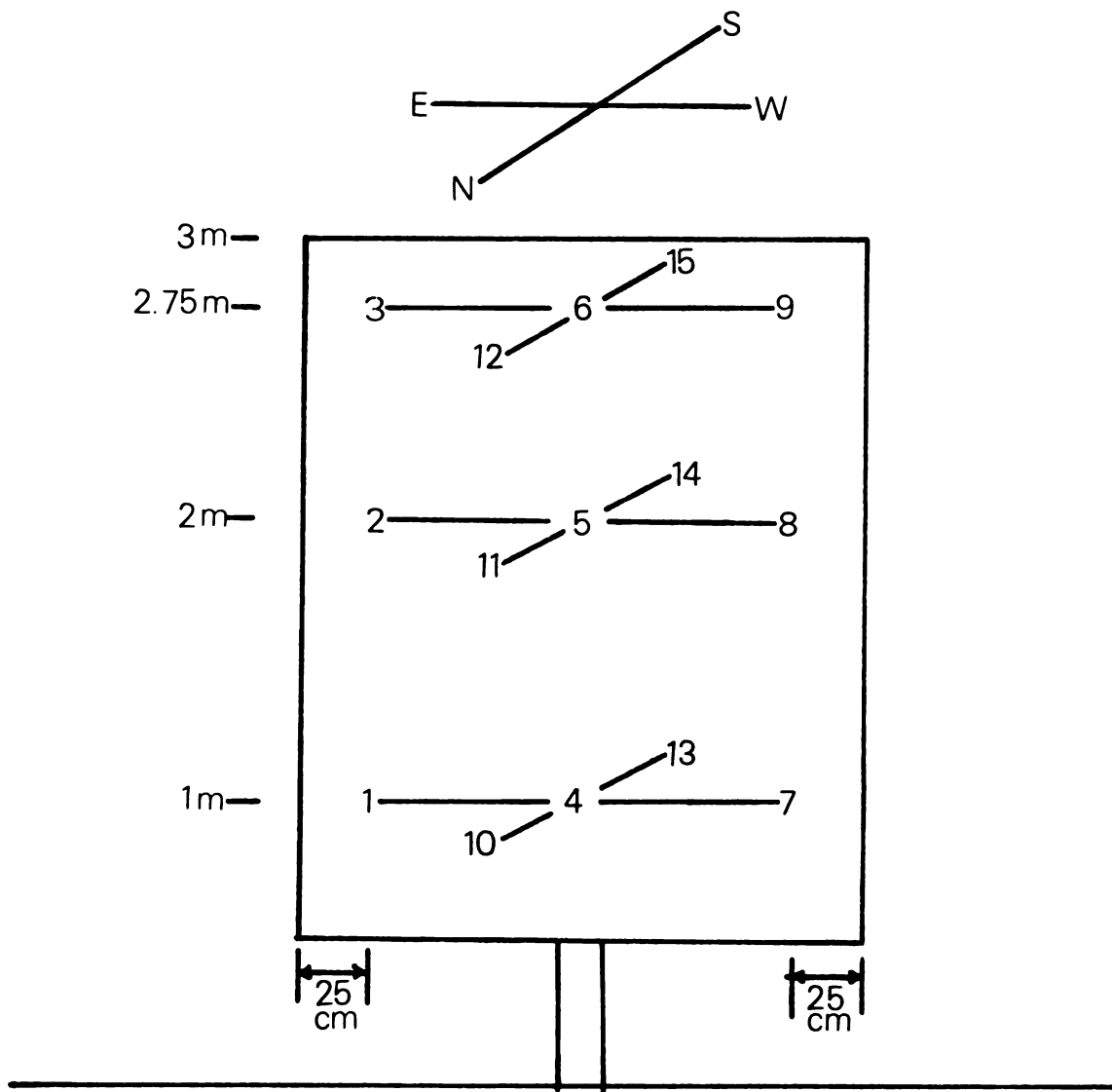


Figure 1. Location of percent sky readings in trees, position 1 to 9, 1978, positions 1 to 15, 1979.

radiation microclimate in 1979 within tree canopies using a technique similar to that of Lakso (36), except that % sky was determined by measuring transmission of light through the negative. Using this technique the following equation was used to calculate % sky.

$$\text{Log \% sky} = 2.03 - 1.0 (\text{Log transmittance, lux})$$

In 1978 the radiation determinations were taken with a Lambda PAR meter. Full sun readings were taken above the tree canopies,

$$\% \text{ Full Sun} = \frac{\text{PAR reading (in canopy)}}{\text{PAR reading (full sun)}} \times 100$$

Determinations were taken at approximately solar noon throughout the 1978 and 1979 seasons on bright, sunny days. Since 1978 and 1979 data were similar only the more detailed 1979 observations will be discussed in depth. Unless otherwise indicated data are expressed as

$$\% \text{ sky} = \frac{\text{Sky (in canopy)}}{\text{Sky (full sun)}} \times 100$$

Spectral Distribution. Spectral distribution of global radiation was determined between 1:00 p.m. and 3:00 p.m. on August 30, 1979, with a spectroradiometer (ISCO Model SR, Lincoln) at 1, 2 and 2.8 m above ground in the center of three 'Harken' trees (6 yrs old, 3 m high) on Siberian C rootstock trained to an open center.

Fruit maturity vs. light intensity. Six trees of 'H 420'/Siberian C planted in 1973 and trained to an open center were used for this study. 'H 420' is a selection from the Harrow breeding program maturing in late August. Sixty-three positions were chosen throughout the tree canopies. Percent sky was determined using hemispherical photography on August 12, 1979, a bright sunny day, when vegetative canopy was fully developed. On August 30, all the fruit within a 25 cm radius of the point where a light intensity reading was taken

on August 12 were harvested and rated visually for maturity according to colour, on a scale of 1 to 5, with 5 being the most mature and 1 the least.

Statistics. Duncan's multiple range test was used for mean separation and multiple regression to determine the relationship between % sky, fruit number and maturity (58).

Results

Before hedging (June 3-4 and June 27) the area with the greatest % sky values for all treatments was the upper 25 cm. (Figure 2). On June 3 and 4 more light was recorded at the 1 m level than at the 2 m level in all treatments except COF. The only treatments on June 27 with increased light at 1 m than at 2 m were MCL and OC. On June 3, 5% less light was recorded at the 1 m than at the 2 m level in COF and this was significantly ($p = .05$) less than the other 3 treatments. Differences between training systems were not significant at 2 or 2.75 m. On June 27 the OC treatment had significantly ($p = .01$) more light than the other 3 treatments at the 1 m level, but differences at other levels were non-significant.

Six days after hedging no regrowth had started. The % sky values did not differ significantly at the 2.75 m and 2 m levels for all treatments, but at the 1 m level MCL and OC had significantly ($p = .05$) higher % sky values than OF (Figure 2, July 18). Only the MCL treatment had higher % sky values at the 1 m level than the 2 m level.

Forty days after hedging (Figure 2, August 21) the zone with the greatest % sky values was again the upper 25 cm. Significantly

Figure 2. The effect of training system, oblique fan (OF) canted oblique fan (COF), modified central leader (MCL), and open center (OC) for hedgerow peaches on mean % sky values during the 1979 growing season. % sky values are the mean of 15 values within the tree.

Figure 2

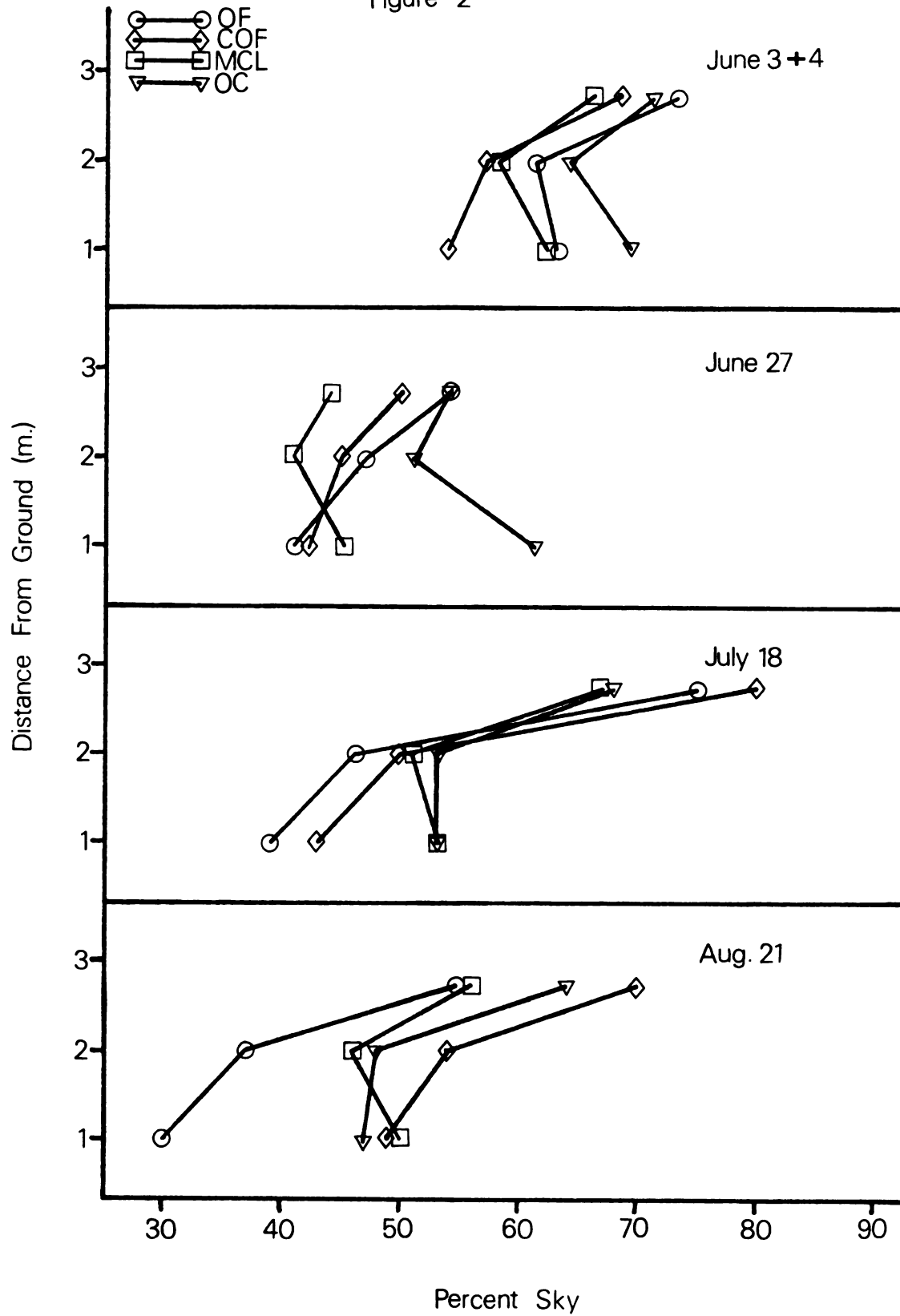


Table 1. Seasonal percent sky determinations at different locations^z within 4 peach training systems

Height ^y (m)	OF			COF			MCL			OC										
	N	S	C	E	W	N	S	C	E	W	N	S	C	E	W					
	June 3 & 4																			
2.75	87	86	60	60	72	65	66	71	72	65	66	77	58	75	54	68	74	77	65	70
2.00	60	66	56	57	64	56	60	57	57	56	65	60	56	45	62	62	72	63	57	67
1.00	55	76	56	59	70	51	55	51	56	56	60	70	54	59	67	68	74	72	62	70
	June 27																			
2.75	58	64	52	38	57	55	55	48	53	34	44	54	37	44	42	37	67	54	54	56
2.00	38	53	45	42	55	49	48	42	39	46	43	47	34	28	55	48	60	49	44	56
1.00	37	48	33	39	46	48	54	41	34	31	51	50	38	37	47	56	67	61	57	64
	July 18																			
2.75	69	73	71	78	86	90	85	98	78	49	70	66	64	69	68	59	63	76	91	49
2.00	38	45	55	39	54	62	51	46	43	50	55	47	45	37	72	41	50	54	53	67
1.00	37	48	33	32	43	43	47	44	53	30	56	59	42	50	60	44	56	61	43	62
	Aug. 21																			
2.75	67	53	42	40	75	89	68	88	56	51	41	52	43	74	68	43	66	86	64	61
2.00	34	40	36	36	40	55	49	46	65	54	42	46	38	40	62	44	53	47	46	51
1.00	26	38	27	27	34	39	67	37	48	54	52	54	41	44	60	41	45	48	47	35

^z% sky determinations 25 cm from edge of tree, except center, mean of 3 trees.

^yHeight from ground.

($p = .05$) less light was recorded at the 2 m and 1 m level in the OF system than in the other 3 treatments.

There was very little difference between % sky levels in the outside 25 cm of the canopy and values in the center of the tree (Table 1).

Spectral distribution of light. As canopy depth increased absorption of radiation of all wavelengths decreased but not equally (Table 2). Light of 400 nm penetrated least and near infrared (750 nm) most. The area of greatest absorption occurred between 2 and 2.8 m above the ground.

Effect of light intensity on fruit maturity. Multiple regression analysis relating % sky, and fruit number with maturity (Table 4) indicated that fruit maturity increased with % sky but decreased with fruit number. Percent sky and fruit number accounted for 40.7% of the variation in the relationship.

Discussion

Proctor et al. (53) observed that little absorption of light occurred on the periphery of apple trees, and that the zone of greatest absorption occurred between 1 m and 2 m from the tree top. This differs from our findings with peach where the greatest absorption occurred in the outer 25 cm (Figure 2, Table 1). Continual hedging results in the formation of dense growth at the top of the tree which absorbs a high percentage of light. This is normally thinned out during dormant pruning, but in 1979 only dead wood was removed. This emphasizes the importance of careful dormant pruning, or the use of a hedging practice that removes wood at different levels

Table 2. Spectral distribution of global radiation ($\mu\text{w cm}^{-2}\text{nm}^{-1}$) above and at various distances from the tree top in a peach tree

Wavelength (nm)	Distance from Ground (m)			Above Tree
	1 (% of above tree)	2	2.8	
400	23	26	68	48.26
450	39	31	83	61.95
500	32	34	79	75.48
550	33	39	88	71.05
660	39	36	87	64.50
675	25	39	78	70.50
730	39	42	82	52.90
750	61	60	88	55.80

to permit proper light penetration into the hedge. In 1978 the trees were properly thinned out during dormant pruning and the % sky determinations before hedging are fairly high, some even at 100% Full Sun (Table 3).

The hemispherical lens used is an equidistant projection lens, and can give higher % sky than % full sun values because of the canopy gaps near the horizon (36). However, in this study there was good agreement ($r = 0.88$) between % sky and PAR values for sunny cloudless days.

In a number of cases, the 1 m level had higher light levels than the 2 m level. Similar results have not been obtained with apples or other crops. Increased light at these lower levels could be attributed to the fact that few new branches are formed at this level, and when present are usually removed during dormant pruning. Increased reflection of light from surrounding trees could account for some of the increase in light levels.

In the COF treatment the lowest readings occurred on June 27. The readings increased after hedging and even continued to increase at the 2 m and 1 m level on August 21. The architecture of the tree combined with the fruit load later in the season opened the canopy and increased light penetration late in the season at the middle and bottom of the canopy.

OF had the lower light levels in a number of cases, especially later in the season, and OF is also the narrowest tree wall at 1.5 m. This is not so surprising when the Leaf Area Index (LAI) is accounted for. Unpublished data (Gaynor, personal communication) for these training systems shows mean LAI for 3 years (1975-77) for OF of 4.57,

Table 3. Seasonal percent Full Sun determinations in 1978 at different locations^Z within peach trees trained to 4 systems^Y.

Training Systems	Date	% Full Sun								
		Position ^X								
		E			C			W		
		1	2	3	4	5	6	7	8	9
OF	6/14	86	74	100	32	43	100	6	70	100
COF	6/20	63	88	72	64	21	92	19	75	66
MCL	6/20	70	50	99	88	84	99	65	62	83
OC	6/23	58	100	88	44	99	99	73	51	89
OF	7/17	20	45	86	4	65	66	24	37	95
COF	7/17	38	67	75	71	67	48	16	7	98
MCL	8/8	25	16	52	42	26	27	33	20	28
OC	8/8	33	50	23	62	66	92	46	74	72

^Z% full sun determinations 25 cm from edge of tree, except Center, mean of three trees, determined by PAR readings.

^YHedged July 1978.

^XPositions refer to positions in Figure 1.

and for COF, MCL and OC 2.92, 3.30 and 2.96, respectively. Heinicke (23) determined that a LAI of ca. 4 to 5 is about the maximum which will allow sufficient light for the maximum photosynthetic rate to strike all foliage. In later work Heinicke (25) determined the LAI for apple trees in 4 size groups as follows, standard, 3.56, semi-standard, 3.09, semi-dwarf, 3.52 and dwarf, 2.94.

When peripheral readings are compared with center readings at all levels and in all treatments, there were no striking differences in light interception within the canopies (Table 1). The lowest reading (25%) occurred August 21 at the 1 m level on the north side in the OF treatment (Table 1). The greatest decrease in most cases occurred from outside the canopy to the reading in the peripheral zone, 25 cm inside the canopy. This would suggest that the majority of the growth occurs in the peripheral zone of peach trees, with very little in the center of the tree, and this is supported by general observations. Thus simple hedging alone will not completely "open" the tree to increase light penetration. The use of a slotted saw (8) or careful dormant pruning will be required to increase light levels in the center of the canopy.

The four training systems are relatively efficient in light interception. The light level required for flower bud initiation in apples is 30% FS (8, 23, 30). Light levels during flower bud initiation were above this level in our study (the optimum level for peach has not been determined) except for the June 27, 2.0 m, E, determination in MCL where the reading was 28% sky (Table 1). However % sky underestimates shading because of the equidistant lens. Light levels for all treatments were high even late in the season.

The changes in the spectral distribution within the open center canopy agrees with reports of others (16, 53). Federer and Tanner (16) suggest that varying light quality may affect growth and photoperiod response, while Proctor et al. (53) suggest that colour development in apple may be dependent on a required spectral distribution. Lavee and Erez (39) concluded that light in the 600–690 m μ range was needed for leaf bud burst in peaches and small amounts in the 500–600 m μ enhanced flower bud burst. Light quality changes are not likely at this time of year since no foliage has yet developed.

Percent sky and fruit number together accounted for 40.7% of the variation in fruit maturity, while each one alone only accounted for 19.2 and 17.3%, respectively, (Table 4). Increasing % sky would have only a small effect on increasing fruit maturity.

Light interception and light levels are very important in fruit production, and determination of light interception patterns is essential in developing training systems and orchards for the future. However, light interception was little affected by training system in this study. The OF system gave the highest yields in 1979, and the highest or second highest yields in 1973 to 1978, with accumulated yields for 1973 to 1979 of 124.6 (OF), 104.2 (COF), 110.6 (MCL) and 92.2 (OC) tonnes per hectare (Layne, unpublished), despite the fact that light levels were consistently lower at the 1 m level after June 27 and significantly lower ($p=.05$) at July 18 (1 m level) and August 21 (1 m and 2 m level). The relationship between light levels and fruit bud formation, fruit set, and fruit growth thus needs to be determined for peach.

Table 4. The effect of percent sky and fruit number on fruit maturity.

Independent variable	Dependent variable	equation of line	r	R ²
percent sky x ₁	maturity y	y = 1.301 + 0.022x ₁	0.438	0.192
fruit number x ₂	maturity y	y = 3.527 - 0.116x ₂	-0.416	0.173
percent sky x ₁	fruit number x ₂	x ₂ = 7.258 + 0.019x ₁	0.103	0.011
percent sky and fruit number x ₁ , x ₂	maturity y	y = 2.873 + 0.025x ₁ - 0.130x ₂	0.638	0.407

SECTION II

EFFECT OF SHADING ON PHOTOSYNTHESIS, SPECIFIC
LEAF WEIGHT, CHLOROPHYLL CONTENT AND MORPHOLOGY OF
YOUNG PEACH TREES

Abstract. One-year-old trees (Prunus persica (L.) Batsch cv. Redhaven) grown under 4 different light intensities did not differ significantly in shoot length, internode length or node number. Heavy shade (9% Full Sun) caused a 24% reduction in average stem diameter. Average leaf areas increased by 18%, 30% and 20% for light (36% FS), medium (21% FS) and heavy (9% FS) shade respectively. Shading caused a more horizontal leaf orientation. Specific leaf weight (11.1 mg cm^{-2} at 100% FS; 4.3 mg cm^{-2} at 9% FS) and photosynthetic rate (23.2 at full sun versus $12.7 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$ at 9% FS) decreased as light intensity decreased. Photosynthetic rate decreased with shading when expressed as mg CO_2 fixed per unit area or per mg chlorophyll per hour, but increased when expressed as amount CO_2 fixed per unit dry weight. Chlorophyll content per unit leaf area increased with shading but stomatal resistance was not affected. Leaves from shade treatments became light saturated between $400\text{--}1100 \mu\text{Em}^{-2}\text{s}^{-1}$; and maximum photosynthetic rates decreased as shade increased.

Tree size, spacing, and training system have a dramatic effect on light conditions within the canopy (60, 26). Heinicke (25) observed that the percentage of the leaf area which received insufficient light for proper growth and reproduction (less than 30% FS) decreased as apple tree size decreased.

The photosynthetic efficiency of leaves in the inner shaded zone of apple trees is about one-third that of those in the outer, full sun, zone (26, 44). However, light compensation point for apple is low and is seldom reached during the day (26). Mika and Antoszewski (44) hypothesized that photosynthesis in apple reaches its maximum at 70% full sunlight.

Barden (2) found no effects of various light levels on apple shoot length, leaf number or total leaf area; however, net photosynthesis, dark respiration and specific leaf weight were higher in sun than in shade leaves. The palisade layer and the leaf itself were thicker in sun than in shade leaves (31).

Photosynthetic rates of 9.5 to $15 \text{ mg CO}_2 \text{ dm}^{-2}\text{hr}^{-1}$ have been reported by Chalmers et al. (10) and Crews et al. (12) for two different peach varieties. Crews reported a light compensation point below 1 mW cm^{-2} of PAR, for sun leaves, while no data have been reported for leaves grown in shade. Light levels this low are seldom experienced in tree canopies during daylight.

This work was undertaken to determine the effects of varying light intensities on photosynthesis, Specific Leaf Weight (SLW), chlorophyll content, growth and morphology of young peach trees.

Material and Methods

One-year-old peach trees cv. Redhaven were planted in 38 l pots in sand: peat: soil (1:1:1 by volume) on May 5, 1979. Fertilizer, pesticides, and water were added as needed. Trees were grown under full sun until June 20, 1979, then placed under shade treatments consisting of 100%, 36%, 21% and 9% of full sun. Shading was achieved by placing trees under polypropylene shade fabric (Glockner, New York, N.Y.) with 4 single tree replicates per treatment. Spectral radiometer determinations confirmed that all wavelengths in the 380-750 nm range were reduced equally.

Morphological data were recorded on September 11 and 12, 1979, and included length of scaffolds and laterals, internode length, node number, stem diameter, and average leaf area of leaves formed after shade treatment was applied, as well as specific leaf weight (of both pre-shade and postshade leaves).

Chlorophyll was determined according to the method described by Arnon (1). Two leaf discs (8.5 mm diameter) were punched from leaves formed in shade and were macerated in 2 ml of cold 80% acetone. After washing twice with 2 ml volumes of 80% acetone the total sample was spun at 5000 rpm for 5 min in a Sorvall refrigerated (0° C) centrifuge model RC2B, head SS34. The pellet was resuspended in 2 ml of solvent and recentrifuged. The combined supernatants were stored in the dark at 0° C. After dilution to a final volume of 8 ml, concentrations of chlorophyll a and b were determined from values obtained at 645 nm and 663 nm with a Beckman spectrophotometer.

Gross photosynthesis and stomatal resistance were measured with a ventilated diffusion porometer (Model VP-1, Cayuga Development,

Ithaca, N.Y.) using the method described by Peet et al. (48). The porometer contained a lithium chloride humidity sensor which allowed estimation of stomatal resistance while exposing the abaxial surface of the leaf (1 cm^2) to $^{14}\text{CO}_2$ ($10.1 \mu\text{l/l}$, 342 ppm CO_2 , 21% O_2 , 14 ml) for 30 sec. Immediately after pulsing, the exposed area was excised with a no. 11 cork borer and placed in a scintillation vial containing 0.5 ml of Protosol (New England Nuclear) and digested for at least 48 hr. Samples were bleached with 1.0 ml of benzoyl peroxide in toluene (5 gm in 30 ml). After 24 hr, 15 ml of scintillation fluid (5 gm PPO/1 toluene) was added and radioactivity was determined with a Beckman LS 100 Liquid Scintillation spectrometer. Corrections were made for background and quenching and gross photosynthetic rate was calculated as $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$, $\text{mg CO}_2 \text{ mg chl}^{-1} \text{ hr}^{-1}$ or $\text{mg CO}_2 \text{ mg dry wt}^{-1} \text{ hr}^{-1}$, by using leaf disc area, exposure time, radioactivity, specific activity of CO_2 , SLW, and chlorophyll values.

Net photosynthesis and light response curves were determined with an open gas analysis system on whole leaves on July 16, 1980, as described by Sams and Flore (55). Determinations were made on the first fully expanded leaf after treatments, $25^\circ \pm 0.5^\circ \text{ C}$, and ambient CO_2 , O_2 and N_2 levels.

Light intensities were determined with a LI-COR Model LI-190S quantum sensor connected to a LI-COR LI 185 Quantum/Radiometer/Photometer (LI-COR inc., Lincoln, NE). Mean separation was determined using Duncan's multiple range test.

Results

The shading treatments did not significantly affect shoot length, internode length or node number although node number was reduced at

Table 1. The effect of artificial shade on gross morphology^z of 'Redhaven' peach.

Sunlight (%)	Shoot Length (cm)	Internode Length (cm)		Node Number	
		Postshade	Pre-shade	Postshade	Pre-shade
100	36.8	1.5	1.9	11.6	13.8
36	44.8	1.7	1.6	11.0	15.8
21	44.0	1.8	1.6	11.9	14.9
9	41.0	1.8	1.5	8.7	16.1

^zNo statistical significant differences.

9% full sun (Table 1). Shading decreased stem diameter, but only heavy shade (9% full sun) had a significant effect (Table 2). Leaf areas (Table 2) increased with shading up to 21% FS, then decreased under 9% FS. Leaf areas increased by 18%, 30% and 20% for 36, 21 and 9% FS respectively. As shade increased branches became more horizontal (Figure 1).

Specific Leaf Weight (SLW) decreased as light intensity decreased for both leaves formed before (pre-shade) and after (postshade) shade was applied (Table 2). In postshade leaves SLW decreased 28, 42 and 61%, in pre-shade leaves 28, 31, and 47% for 36, 21 and 9% full sun, respectively.

Chlorophyll content in leaves formed after shade was applied increased as light decreased whether expressed on the basis of surface area or dry weight (Table 3). Treatments were significantly higher than 100% FS for chlorophyll a, b and total chlorophyll. The ratio of chlorophyll a to b was not significantly affected by shading.

The photosynthetic rate, (expressed on an area basis), of postshade leaves decreased as shading increased but only the 9% FS differed significantly from the control (Table 4). No statistical differences existed between pre-shade leaves. When the photosynthetic rate of the postshade leaves was expressed on a mg chlorophyll basis the rate decreased as shading increased, but when expressed on a mg dry weight basis it increased.

Stomatal resistance was not significantly affected by shading. Light saturation occurred around $1100 \mu\text{E m}^{-2} \text{s}^{-1}$ for 100% FS leaves while 9% FS leaves became saturated between 400 and 600 $\mu\text{E m}^{-2} \text{s}^{-1}$ (Figure 2). The light compensation point was very low (below

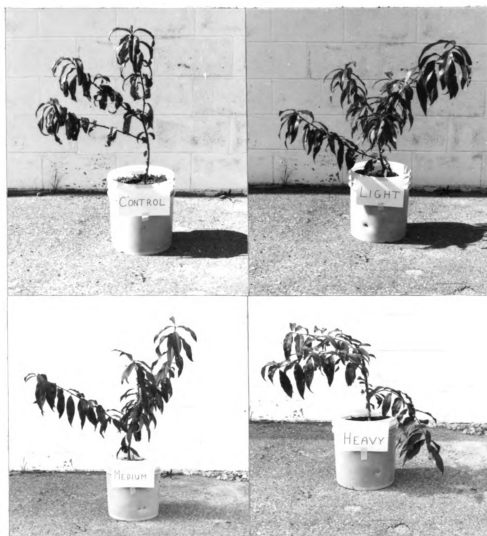


Figure 1. The effect of shade on branch angles of young peach trees.
Control = 100% FS; Light = 36% FS; Medium = 21% FS;
Heavy = 9% FS.

Table 2. The effect of artificial shade on scaffold stem diameter, average leaf area of postshade leaves and specific leaf weight of pre- and postshade leaves of 'Redhaven' peach.

Sunlight %	Stem diameter (mm)	Mean leaf area (cm ²)	Specific leaf weight	
			Pre-shade (mg cm ⁻²)	Postshade
100	4.1a ^z	29.6a ^z	11.1a ^y	10.1a ^y
36	3.9ab	34.9ab	8.0 b	7.4 b
21	3.6ab	38.6 b	6.4 bc	7.0 b
9	3.1 b	35.6ab	4.3 c	5.4 c

^zMean separation within columns by Duncan's multiple range test 5% level.

^yMean separation within columns by Duncan's multiple range test 1% level.

Table 3. The effect of artificial shade on chlorophyll content of postshade leaves of 'Redhaven peach.

Sunlight (%)	Chlorophyll a	Chlorophyll b	Total chlorophyll	a/ b
	mg.dm ⁻²			
100	2.85a ^z	1.32a	4.18a	2.16
36	4.90 b	1.74 b	6.64 b	2.82
21	4.82 b	2.16 c	6.97 b	2.23
9	5.25 b	2.49 c	7.74 b	2.11
	mg chlorophyll / mg dry wt (x 10 ⁻³)			
100	2.56a	1.20a	3.76a	2.13
36	6.13 b	2.18 b	8.32 b	2.82
21	7.12 b	3.38 c	10.90 b	2.11
9	12.10 c	5.74 d	17.90 c	2.11

^zMean separation within columns by Duncan's multiple range test 1% level.

Table 4. The effect of artificial shade on photosynthetic rate^w and stomatal resistance of post and pre-shade leaves of 'Redhaven' peach.

Sunlight (%)	Photosynthetic Rate			Stomatal Resistance	
	Pre-shade (mg CO ₂ dm ⁻² hr ⁻¹)	Postshade (mg CO ₂ /mg Chlorophyll hr ⁻¹)	Postshade (mg CO ₂ /mg dry wt hr) (x 10 ⁻²)	Pre-shade (s.cm ⁻¹)	Postshade (s.cm ⁻¹)
100	18.8 ^z	23.2a ^y	5.64a x	2.08a ^y	4.94 ^z
36	22.2	22.7a	3.44 b	2.82 b	4.36
21	20.6	19.7a	2.80 bc	3.06 b	4.76
9	16.5	12.7 b	1.66 c	2.96 b	5.26
					7.90

^zNo statistically significant differences.

^yMean separation within columns by Duncan's multiple range test 5% level.

^xMean separation within columns by Duncan's multiple range test 1% level.

^wBright sunny day, temp. 24° C.

Figure 2. The effect of artificial shade on the photosynthetic rate of leaves of 'Redhaven' peach under varying light levels. These are representative curves and each point is the mean of 2 leaves per tree.

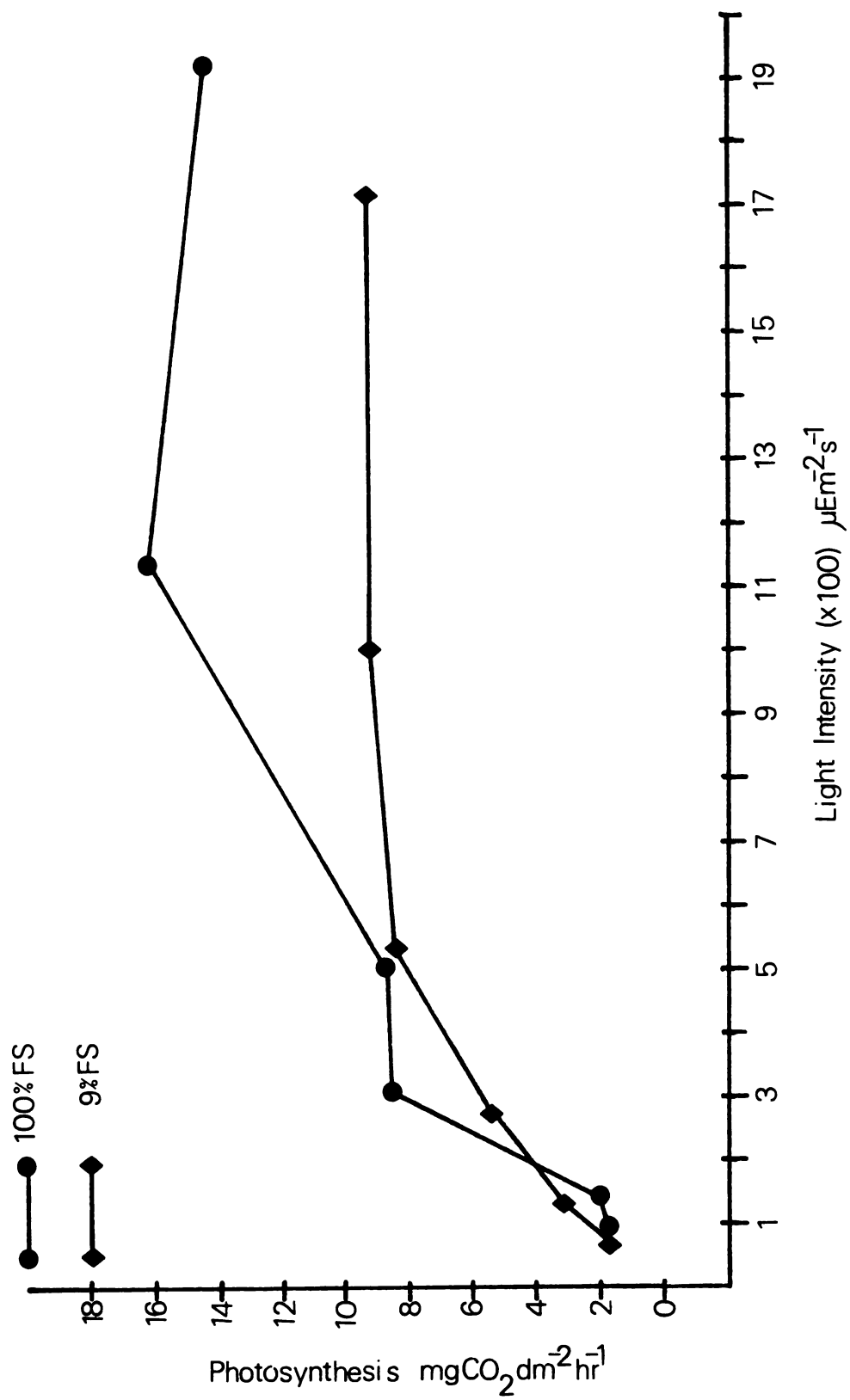


Figure 2

100 $\mu\text{E m}^{-2} \text{ s}^{-1}$) for both treatments.

Discussion

Shading decreased stem diameter with only the 9% FS treatment causing a significant difference. Average leaf area increased with decreasing light down to 21% FS treatment. The increase of leaf area was also found in apple along with other morphological changes. Maggs (43) observed that shading of apple leaves reduced length of new stems, number of leaves, internode length and total leaf area, while individual leaves had the greatest area in intermediate shade (41% FS) and the greatest weight in full light. Priestley (50) found that shade (1/3 and 1/10 daylight) increased specific leaf area in apple. Jackson and Palmer (32) reported that shading reduced the number and weight of new apple shoots, the fresh weight per unit length of shoot, girth increment and leaf thickness and weight per unit area. In the present work increasing shade did not result in as many morphological changes but leaves and branches were more horizontal. Leaves under heavier shade grew larger, which resulted in an increase in their effective light interception area.

The Specific Leaf Weight (SLW) in apple was reduced by low light (2). We obtained similar results for leaves formed both before and after the shade was applied. Barden (2) hypothesized that SLW might be a useful index of previous light exposure and photosynthetic potential.

The chlorophyll content (Table 3) increased with decreasing light intensity in our studies. Gabrielsen (18) determined that the effect of the chlorophyll on photosynthesis reaches its optimum at a concentration of 4 to 5 mg (a + b)/dm², and hypothesized that an increase in

concentration beyond this limit would not affect the rate of photosynthesis. This level was reached in all of our treatments. Boardman (4) suggested that shade leaves contain more chlorophyll. Leaves grown at low light intensities have more chlorophyll per unit weight or unit volume of leaf, but the chlorophyll content per unit area of leaf surface is very often lower than that of leaves grown at higher light intensities. Our data supports Gabrielsen's hypothesis, increases in chlorophyll did not increase photosynthesis. This study does not totally agree with Boardman, chlorophyll increased with decreasing light on both an area and dry weight basis in the peach leaves sampled in this study.

As chlorophyll content increased photosynthetic rate on an area basis decreased. On a dry weight basis both the rate of CO₂ assimilation and chlorophyll content increase as light decreased. CO₂ assimilation per unit chlorophyll decreased as light decreased, suggesting that the chlorophyll in shade leaves was not as efficient as that in sun leaves. Buttery and Buzzell (5) noted a positive correlation between the photosynthetic rate and chlorophyll content in a number of soybean varieties. They hypothesized that there is a direct causative relationship between quantity of chlorophyll and rate of CO₂ assimilation and that under field conditions chlorophyll content limits photosynthesis. Shading reduces the thickness of palisade tissue in apple leaves (31). In woodland strawberry the amount of mesophyll tissue increased as light intensity decreased (6). In two legume species sun leaves are thicker than shade leaves (11) due to both a larger number and a greater size of palisade and mesophyll cells. The palisade layer of sun leaves was more clearly differentiated than in shade leaves.

Boardman (4) suggests that mesophyll resistance, which is usually taken to be the sum of the biophysical and biochemical resistance to CO₂ movement between the mesophyll cell wall and the site of carboxylation in the chloroplast, is higher at low light intensity. The reduced differentiation of palisade and mesophyll cells and the increased mesophyll resistance in leaves grown under lower light levels would reduce photosynthetic rate while increasing chlorophyll content. As noted above, photosynthetic rate decreased while chlorophyll content increased under shade.

The photosynthetic rate of woodland strawberry leaves expressed on a dry weight basis increased as light intensity decreased (6); the same relationship held for peach in our work.

As light intensity decreased, photosynthetic rate decreased but chlorophyll content increased. This data suggest that chlorophyll content does not limit photosynthesis in shade leaves. Other factors such as leaf morphology, chloroplast structure, mesophyll resistance or RuDP carboxylase activity may be limiting photosynthesis in these stressed leaves.

The light compensation point for both the 100% FS and 9% FS leaves was very low (below 100 $\mu\text{E m}^{-2} \text{s}^{-1}$). It is unlikely that this point is reached in a peach tree on a bright sunny day. The maximum rate of photosynthesis was much lower for 9% FS than for 100% FS (Table 4, Figure 2). The rate of CO₂ assimilation of leaves growing on the inside of a peach tree (at lower light levels) would be lower than leaves growing at the top of the tree, even though the former would be operating at their maximum photosynthetic rate. Crews et al. (12) reported that photosynthetic rate for peach leaves

increased linearly with light intensity from 5.4 to a maximum of 9.6 mg CO₂ dm⁻² hr⁻¹. The photosynthetic rate varied throughout the tree from 3.6 to 12.5 mg CO₂ dm⁻² hr⁻¹. The preconditioning light levels for the leaves used were not indicated. Chalmers et al. (10) measured photosynthetic rate throughout peach tree canopies and found differences between layers. Again the preconditioning light levels, which would determine the maximum potential photosynthetic rate of each leaf, were not recorded. A leaf growing low in the tree would have a lower maximum photosynthetic rate than a leaf from the upper, outer edge, even if both were light saturated.

Summer hedging, by increasing the light levels in those areas, may or may not increase the photosynthetic rate of leaves growing in the lower portions of the tree depending on whether light intensity is saturating at these lower levels. The tree should be trained and pruned in such a way as to maintain high levels throughout the growing season, so that shading does not lower the maximum potential photosynthetic rate.

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APPENDIX

Appendix 1. The effect of training system, oblique fan (OF), canted oblique fan (COF), modified central leader (MCL), and open center (OC) for hedgerow peaches on mean % sky values during the 1979 growing season, with mean separation. % sky values are the mean of 15 values within the tree.

Distance from Ground	Oblique Fan	Canted Oblique Fan	Modified Central Leader	Open Center
(m)				
		June 3 & 4		
1	63 b ^z	54a	62 b	69 b
2	61	57	58	64
2.75	73	68	66	71
		June 27		
1	41a	42a	45a	61 b
2	47	45	41	51
2.75	54	50	44	54
		July 18		
1	39a	43ab	53 b	53 b
2	46	50	51	53
2.75	75	80	67	68
		Aug. 21		
1	30a	49 b	50 b	47 b
2	37a	54 b	46 b	48 b
2.75	35	70	56	64

^zMean separation within rows by Duncan's multiple range test 5% level.

Appendix 2. Standard deviations of seasonal percent sky determinations at different locations within 4 peach training systems (Table 1, Section I).

DATE	OF	COF	MCL	OC
June 3 & 4	14.57	14.72	11.53	11.04
June 27	15.63	16.62	11.67	13.98
July 18	20.55	22.96	17.56	18.15
Aug. 21	17.60	21.95	15.94	17.13

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