Light Thresholds for Apple Tree Canopy Growth and Development

Curt R. Rom¹

Department of Horticulture and Forestry, University of Arkansas, Fayetteville, AR 72701

Understanding canopy development of fruit trees is important to their management. The tree canopy physically supports the fruit crop. The leaf canopy intercepts light and produces carbohydrates used in growth and metabolic activity. Light distribution within the canopy affects fruit color and quality, and the rate and timing of canopy development affects pest infestation and control. Ultimately, then, canopy development relates to crop quantity and quality and, thus, economic yield of an orchard. The challenge to horticulturists is to manipulate and manage the tree canopy to maximize economic production.

Light is an important aspect of canopy studies because of its role in photosynthesis, its function in developmental morphology of leaves and shoots, its role in flower initiation and fruit set, and its importance to fruit development and quality. Because effects of light can be influenced by the tree training system, pruning, or other mechanical means, such as shading, the question arises, How much light is needed to maximize orchard performance? The purpose of this paper is to review some of the relationships of light to apple tree physiology and performance.

Two aspects of light and tree canopy development must be considered. First, interception of available light by the total orchard canopy is correlated to total biomass production of the crop system (Monteith, 1977). Second, penetration and/or distribution of light within a single tree canopy must be optimized for maximum tree performance and crop development.

Light interception

Light interception is the amount of available light intercepted by the tree canopy and not striking the orchard floor. Interception, then, is a function of plant density, canopy shape and size, and leaf area index (LAI, m² leaf area/m² ground area) within the canopy. This subject has been reviewed in regard to modeling plant growth and response by Thornley (1976) and in specific detail for fruit tree orchard systems by Jackson (1980).

Orchards are a discontinuous canopy with either individual tree canopies or canopy hedgerows with space between trees or rows providing access for labor, machine movement, etc. Thus, the area of open orchard floor is inversely proportional to tree canopy surface. Light intercepted by the orchard floor is obviously not used by the tree.

The amount of light intercepted by the tree is affected by canopy size, leaf surface area within the canopy, and row orientation. Canopy size in turn is related to tree age and training system. Jackson and Palmer (1980) mathematically modeled light interception by fruit trees. The models predicted increased light interception with increasing tree height, canopy width, or leaf area density and reducing alleyway width. Wertheim et al. (1986) reported light interception by trees was linearly proportional to tree density across two trees training systems at two sites and with two cultivars. Light interception ranged from 57% to 81% available light, varied with orchard site due to tree size and cultivar differences, and was reduced by summer pruning. Accumulated production of the systems was quadratically related to light interception with maximum yield at $\approx 75\%$ to 80% light interception. Palmer and Jackson (1974) reported that production in a young high-density orchard increased linearly with increasing light interception between 20% and 60%.

During orchard establishment in various training systems, early production was correlated to total light interception (Barritt et al., 1991). For young trees, light interception was an effect of tree density and canopy size. This issue is discussed further by Barritt et al. (1991).

Because of the need for a clear alley for equipment movement and for light to strike the canopy sides, $\approx 70\%$ to 80% interception may be a theoretical maximum for orchard systems at maturity (Jackson and Palmer, 1972; Jackson, 1980). Orchard systems, such as a full-field (Wertheim et al., 1986) or meadow orchard (Hudson, 1970) that have no alleys may intercept substantially more light than conventional systems. These complete canopy systems, however, would require special equipment for management and harvest (Jackson and Palmer, 1980).

Canopy design and shape influence light interception. Jackson and Palmer (1972, 1980) modeled the influence of canopy shape on interception and validated the models using solid, scale models (Jackson and Palmer, 1979). Interception was proportional to the area of ground covered by the tree and the hedge height in relation to clear alleyway. Interception was more dependent on the horizontal than vertical components of tree size. Wertheim et al. (1986) compared single, and multiple-row beds of trees trained to two systems. Light interception of the systems differed only 3%, with the taller and wider trees intercepting more light. Multiple-row beds two to four rows, however, intercepted 10% more light than single rows.

Pruning generally reduces total light interception because of reduced growth and canopy size. Summer pruning has been shown to improve light penetration within tree canopies (Marini and Barden, 1987), but the effects on light interception are not as well documented. Summer pruning in combination with dormant pruning reduced light interception by 15% (Wertheim et al., 1986).

Light interception varies during a season due to leaf surface area development and solar angle, and during orchard establishment due to tree size increase. Light interception during the season closely follows leaf area development (Palmer, 1974; Palmer and Jackson, 1977). Although LAI was maximized by the middle of the growing season (mid-July), light interception continued to increase until harvest, presumably due to canopy spread from fruiting. Total light interception by north-south rows did not vary after complete canopy formation (Jackson and Palmer, 1972). East-west rows were inefficient at midseason light interception but, because of solar angle, tall east-west hedgerows intercepted more light than north-south hedgerows at higher latitudes during early and late summer.

Light interception is typically expressed as percentage of available light. Reporting interception or irradiance as percent full sun is useful for comparisons within a single experiment but does not allow comparisons in time or space and the evaluation of energy input requirements for cropping. Some preliminary relationships between light quantum or energy interception and crop production are discussed by Robinson et al. (1991).

Light penetration and distribution within canopies

Light intensity decreases within the tree canopy (Barritt et al., 1987b; Heinicke, 1963; Looney, 1968) as the outer portion shades the inner canopy. In eastern Washington, light in mature, central-leader-trained 'Delicious' apple trees sharply decreased inside the first 0.5 to 1.0 m from the canopy edge (Fig. 1). In the bottom of 4-m-tall trees, light was reduced to 8% to 10% of full sunlight (Barritt et al., 1987b). Smaller trees have less canopy volume than full-sized trees, and thus a smaller proportion of the total leaf area at light levels $<30\%$ of full sun (Heinicke, 1964).

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¹Associate Professor, Dept. of Horticulture and Forestry, College of Agriculture, Univ. of Arkansas, Fayetteville.

Fig. 1. Light intensity decreases from the top of the tree canopy to the interior bottom of the canopy. Graph represents data collected from six replicate 'Delicious' trees in eastern Washington.

Light transmittance through the canopy decreases with increasing LAI (Heinicke, 1963) and follows Beer's Law (Jackson, 1980). Transmittance is a logarithmic function of the LAI, of the distance through the canopy that the light penetrates and depends on incoming light intensity. Measured light may be higher than indicated by the model due to the proportion of diffuse or reflected light, the leaf arrangement in that space (e.g., clumping vs. evenly distributed) and the distribution of leaf angles.

The light environment within the canopy is not uniform. Portions of the inner canopy may receive high light intensities at times due to sunflecks penetrating the canopy or changes in solar position during the day. Thus, sections of the canopy may receive high light for a brief time and predominantly low light for the remainder of the photoperiod. Similarly, the proportion of direct vs. diffuse light changes with diurnal changes in the light intensity (Lakso, 1975).

Since light levels vary within the tree canopy, and intensity is often at levels significantly below full sun, the question then arises, Does irradiance below full sunlight affect tree growth and development? Maggs (1960) demonstrated that total dry weight of small, potted clonal MM.106 trees was reduced curvilinearly by four shading levels (100%, 78%, 41%, and 24% full sun). The calculated net assimilation rate (mg dry wt/cm² leaf area per day) of the trees was reduced directly with available light. Shading has the greatest effect on tissues not involved in carbon fixation, primarily roots (Den Herder and Rom, 1989; Maggs, 1960; Priestly, 1969). The relation of light to dry weight accumulation is the basis for the relationship between light interception and growth discussed earlier.

Net photosynthesis (Pn) of individual apple leaves increases asymptotically with increasing irradiance to 1000 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ (400 to 700 nm) above which level there is minimal change in Pn (Fig. 2) (Den Herder and Rom, 1989; Lakso and Seeley, 1978). The curve is characteristic of many C3 plants and can be described mathematically in several forms (Thornely, 1976; Thorpe et al., 1978). Pn is considered saturated at 90% to 99% of the maximum Pn ($P_{n_{\text{sat}}}$) and is estimated by regression of the light response. Saturation occurs at 700 to 1100 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ or $\approx 30\%$ to 45% of full sun, although the latter expression is not an accurate description of light quantity.

The Pn rate of apple trees is also affected by previous conditions, by biotic factors (pests and disease), by abiotic factors (temperature, vapor pressure), and by tree cultural practices (water relations, nutrition, pesticides, etc.). Factors affecting photosynthesis have been previously reviewed by Barden (1978), Ferree (1978), and Lakso and Seeley (1978). The saturation point and Pn rate vary with environment in which the leaf develops and leaf type. Leaves developing at lower light levels have lower Pn and lower saturation points. $P_{n_{\text{sat}}}$ and saturation point were decreased by shading young potted apple trees (Table 1; M. Den Herder and C.R.R., unpublished data). This result confirms work by others (Avery, 1975; Barden, 1974, 1978). Although shading decreases Pn on an area basis, when calculated on a dry weight basis, Pn of shaded and exposed leaves is similar. This result implies that leaf morphology and development are sensitive to low light (Jackson and Beakbane,

1970) but the photochemical mechanisms are less affected. Thus, light usage by leaves developing in light-limited regions of the tree canopy may be more efficient than generally considered.

Extension shoot leaves on the outer portion of the canopy develop at higher irradiance than canopy interior leaves (Table 2). Consequently, the Pn rate of shoot leaves is greater than that of watersprouts in the tree center, although of similar age and leaf type. Marini and Barden (1982b) reported a similar trend for spur leaves from the canopy periphery vs. the canopy interior. Summer pruning improved light penetration into the tree canopies (Marini and Barden, 1982a, 1987) and increased Pn of interior spurs (Marini and Barden, 1982b).

Leaves of an apple tree differ in Pn according to leaf type (e.g., fruiting spur, vegetative spur, or extension shoot). Fruiting spur leaves have significantly lower rates of Pn than shoot leaves (Fig. 2, Table 3). Differences in Pn rate have been attributed to leaf morphology because spur leaves have a narrower palisade cell region with fewer palisade layers (Ghosh, 1973). Pn of spur leaves also appears to become saturated at lower irradiance than shoot leaves (Fig. 2). This difference may be an ecological adaptation of the leaves as they normally develop on the canopy interior and would be exposed to lower light levels (Fig. 1).

Photosynthetic response of the whole tree canopy is similar to an individual leaf (Lakso and Seeley, 1978). Individual limb (Landsberg et al., 1975) and whole tree Pn (Sirois and Cooper, 1964) increased hyperbolically with increasing light. Small, whole trees (Crispin/M.27) under field conditions had an exponential increase in Pn with increasing light (Palmer and Rom, 1986). However, whole tree Pn did not appear to be saturated at intensities $>1700 \mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$. Since light penetration and distribution are a function of LAI and canopy depth, the whole-canopy saturation of Pn will vary with tree shape, LAI, and light environment in which the canopy developed.

Ferree (1983) reported that training systems with the lowest light levels within the tree canopy had lower yield efficiency than systems with higher levels. The yield reductions could have been due to reduced flower bud formation and/or fruit set. Shading trees or limbs in one season reduced flower formation and fruit set the following season when trees or limbs were not shaded (Auchter et al., 1926; Jackson and Palmer, 1977; Rom, 1989). Flower bud initiation was proportional to light exposure when whole trees were shaded (Jackson, 1975; Jackson and Palmer, 1977). Shading to

Table 1. Net photosynthesis (Pn) characteristics of 'Delicious' apple leaves grown at various levels of low light in a greenhouse.

Photon flux ^y ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	$P_{n_{\text{sat}}}$ ^x ($\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$)	Pn (mg CO ₂ /h)		
		Per dm ² leaf	Per g leaf	Leaf wt/area (mg·cm ⁻²)
276	1093	22.4	27.7	8.1
104	653	17.9	35.1	5.1
		*	*	*

^z'Topspur Delicious'/M.111 grown in pots in a greenhouse and shaded to various light conditions. Six single-tree replicates of each treatment.

^yPhoton flux for treatment conditions and Pn saturation at 400 to 700 nm.

^xEstimated Pn saturation = photon flux at which Pn was 0.99 of maximum.

*Significantly different by F test, $P = 0.05$.

Table 2. Light environment, net photosynthesis (Pn), and leaf characteristics of a vegetative extension shoot on the canopy exterior and a watersprout shoot on the canopy interior.

Shoot type	PFD ^z	Pn (mg CO ₂ /dm ² per hour) ^y		Leaf area (cm ²)		Chl ^a (μg·cm ⁻²)
		Ambient	Saturated	Avg.	Total	
Extension	1610	21.3	21.3	27	704	74
Watersprout	540	6.7	10.9	17	512	34
	*	*	*	*	*	*

^zPFD = Photon flux density, 400 to 700 nm, in the immediate vicinity at which shoots were growing.

^yPn = net photosynthesis measured at ambient or saturated PFD.

^xChlorophyll a + b.

*Significantly different by F test, $P = 0.05$.

Fig. 2. Net photosynthesis (Pn) saturation point and maximum rate as affected by leaf type. ---, Spur leaves; —, Shoot leaves. Graph represents data collected from five replicate trees of 'Golden Delicious' apple with three subsample leaves per tree per leaf type.

Table 3. Net photosynthesis (Pn), transpiration (Tr), and conductance (g_s) of apple variation with leaf type^a.

Leaf type	Pn (mg CO ₂ /dm ² per hour)	Tr (g H ₂ O/dm ² per hour)	g_s (cm·s ⁻¹)
Extension shoot	28.2 a ^b	4.4	0.687 a
Vegetative spur	27.5 a	4.8	0.627 a
Fruit spur with fruit	23.8 b	4.2	0.545 b
Fruit spur without fruit	24.4 b	3.7	0.526 b
		NS	

^aMeasured on 'Delicious', means from eight single-tree replicates with three sample leaves per replicate.

^bSignificant difference between means with columns by LSD, $P = 0.05$. NS = no significant difference.

levels between 11% and 100% of full sun reduced fruit set proportionately (Jackson and Palmer, 1972). Similarly, fruit set was reduced linearly ($r^2 = 0.90$) with light level (6% to 54% full sun) within mature tree canopies (B.H. Barritt and C.R.R., unpublished data). When single limbs were shaded to 33% full sunlight, fruit set was reduced 20% to 40% compared with nonshaded limbs (Rom, 1989). Shading was effective only when done during the 45-day period after bloom, after which it had no effect. Shading whole trees for periods as short as 3 days during the post-bloom period reduced set (Byers et al., 1990), and the authors suspected that cloudy periods during this time would affect fruit set. Shading individual limbs of mature trees did not reduce fruit set to the extent of shading whole trees (Byers et al., 1985, 1990). This difference indicates intertree transport of carbohydrates and thus a compensation ability of the tree to partially overcome light limitation in shaded portions of the tree, provided other sections are well exposed.

If economic returns were based solely on the volume of fruit produced, then the relation of light to flowering and fruit set would be a primary concern. However, fruit size, color, and sugar content (soluble solids concentration, SSC) are important fruit quality factors of production. Since these three aspects of fruit development all depend on carbohydrates from photosynthesis, they are also responsive to light. Fruits themselves photosynthesize; this aspect has been recently reviewed (Blanke and Lenz, 1989).

Fruit size is smaller in areas of the tree where light is limited (Heinicke, 1968; Barritt et al., 1987b). Fruit weight and SSC were reduced linearly by shading (Robinson et al., 1983). When Heinicke's (1968) data for fruit redness were plotted against light level, a strong linear relation was observed. Barritt et al. (1987a) have presented evidence that fruit redness and SSC of a red-color mutant sport of 'Delicious' increased asymptotically with light penetration into the tree canopy, with maxima for color and SSC occurring at 70% to 80% and 60% of full sun, respectively. Similarly, Tustin et al. (1988) showed a quadratic increase of fruit weight and SSC for 'Granny Smith' up to 50% of full sun, but greenness was negatively correlated to percent light transmission within the canopy.

Preliminary evidence suggests that, although fruit size increased linearly in response to light environment, fruit epidermal chlorophyll content exhibited a quadratic response, with maximum apparent greenness observed between 30% and 60% of full sun and decreasing at irradiances above 60% of full sun (Izso and Rom, 1989).

Conclusion

The question was posed in previous pages as to how much light is necessary for maximum orchard performance. This brief review shows that the question is difficult to answer. To maximize fruit production, light interception by an orchard and distribution within a canopy must be optimized. Total tree dry weight per hectare would certainly be maximized near 100% total light interception. However, this would not permit normal orchard operations with current technologies. Systems with complete light interception may have limiting light conditions within the tree canopy because of between- and within-tree shading (Palmer, 1974). Light interception for fruit production and tree management is optimized at $\approx 70\%$ to 80% of available light. Some new training systems are being studied that may increase this level without limiting light penetration or orchard management. Since interception is a function of tree planting density, canopy dimension, and LAI, interception is optimized by management of these factors. For each cultivar-rootstock-site combination, tree density must be established to allow trees to rapidly fill allotted space in the planting during orchard establishment and attain 70% to 80% interception. Canopy dimensions of tree width and height must be established to intercept light without shading adjacent trees or causing shade in the canopy interior. To maximize interception within a given season, the canopy must achieve optimum LAI soon after budbreak.

Once intercepted, light penetration and distribution within the tree may limit growth and production. Because of the tree's adaptive capacity for Pn, a minimum light level is difficult to determine although maximum Pn clearly occurs at 900 to 1100 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ [45% to 55% of full sun (2000 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ = full sun)] and maximum Pn of leaves that developed in very low light still occurs around 500 to 600 $\mu\text{mol}\cdot\text{s}^{-1}\cdot\text{m}^{-2}$ (25% to 30% of full sun).

Inadequate light penetration and within-tree shade can limit yield by reducing fruit number, size, and quality. An optimum light level of near 70% full sun may be necessary to maximize the most sensitive quality criterion, fruit color. The economic effects of variation in fruit tonnage, size, and quality must be evaluated then to determine the most limiting factor; then, in turn, minimum light levels could be established for maximum returns. From models of light penetration within canopies (Jackson, 1980; Fig. 1) tree widths > 2 m may result in light-limited flower formation, fruit set, and fruit quality. Canopy width and height should be adjusted according to ambient maximum irradiance and latitude of the orchard location.

The common method of expressing units of light in the literature of fruit tree physiology is percent of full sun. However, this is not descriptive of either irradiance flux at a point in time or total irradiation over time. Comparisons between experiments and regions are consequently difficult to make and conclusive generalities are hazardous. Researchers should be aware of the importance of documenting and reporting appropriate units of light flux and total light absorbance or interception.

Some questions regarding light and canopy development need further research. The solar energy requirements for fruit production have not been well established. The diurnal changes of light within a canopy, changes in light quantity and quality during a season, and the relationship to fruiting and fruit quality have not been well studied. Light interception and penetration models have not been validated in orchards.

The focus of most light research in fruit tree canopies has been the role of light in the 400 to 700 nm range. Light of higher and lower wavelengths may have important impacts on morphology, development, and fruit quality. For example, ultraviolet light is important in fruit red color pigment development (Sielgelman and Hendricks, 1958; Walter, 1967); infrared heating (Bergh et al. 1980) and ultraviolet exposure cause fruit solar injury (Simpson et al.,

1988; M.E. Patterson, personal communication). The proportion of these wavelengths relative to photosynthetic wavelengths, their penetration and distribution within the canopy, and their effects require additional research.

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