

**CANOPY LIGHT ENVIRONMENT INFLUENCES APPLE LEAF PHYSIOLOGY  
AND FRUIT QUALITY**

by

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# **Canopy Light Environment Influences Apple Leaf Physiology and Fruit Quality**

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(ABSTRACT)

Several experiments were conducted to determine: the influence of canopy position, girdling, and defoliation on nectar production; whether instantaneous light measurements yield reliable estimates of cumulative seasonal light levels within the canopy; and the effect of the canopy light environment on spur leaf physiology and fruit quality. Defoliation of nongirdled flowering spurs had no effect on nectar production or composition, while defoliation of girdled spurs reduced nectar sugar concentration by 24%. Canopy position had no influence on nectar production or composition. At full bloom there were differences in photosynthetic potential of spur leaves from different canopy positions. Exterior leaves had a greater maximum photosynthetic rate and an unique photosynthetic light response curve compared to the intermediate and interior leaves. Differences among positions persisted throughout the season. Stomatal conductance, specific leaf weight, dark respiration, and light levels were greater for the exterior leaves throughout the season.

Instantaneous light measurements made on a single uniformly overcast day after the canopy was fully-developed (average of four times during the day) provided

reliable estimates (predictive  $R^2 > 0.90$ ,  $n = 30$ ) of total cumulative seasonal photosynthetic photon density (PPD). There was a 1-to-1 relationship between instantaneous and cumulative PPD after canopy development was complete providing both measures were expressed as a percentage. The relationships were equal over multiple dates for two consecutive years. Cloudless conditions provided poor estimates (predictive  $R^2 = 0.49$  to  $0.80$ ,  $n = 30$ ). Light environment and harvest date influenced fruit quality characteristics within the canopy. Fruit red color, intensity of red color, and soluble solids concentration were all positively related to light level, with the highest  $R^2$  on the early harvest dates. Fruit weight, firmness, length/diameter ratio, starch index, and seed number were not consistently influenced by the light environment. The number of hours above an average photosynthetic photon flux density threshold of  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  explained slightly more of the variation in fruit quality characteristics than any other expressions of light.

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## **Introduction**

Light environment influences both the gas exchange characteristics of the leaves within an apple canopy, and fruit quality characteristics such as red color development, fruit weight and soluble solids concentration. However, much of the current understanding of the influence of the light environment on leaf and fruit physiology is the result of research using imposed-shade treatments. These studies have helped to define the basic relationships between light and leaf and fruit physiology, but imposed-shade treatments are not representative of the natural shade conditions within the canopy. With the trend towards higher-density apple plantings, and the possibility of greater within- and between-tree shading, there is a need for research on the influence of ambient light levels within the canopy on leaf and fruit physiology.

Most of the previous studies relating ambient canopy light levels with leaf and fruit physiology were conducted in the arid pacific northwest region of North America, or in other arid regions with predominantly cloudless conditions during the growing season. Sky conditions (cloud cover, pollutants, and haze) interact strongly with the ambient light environment by influencing the relative levels of diffuse and direct light. Changes in diffuse light levels could alter the canopy light environment due to increased light penetration. Thus, humid regions with appreciably more haze and/or cloud cover during the growing season (such as the Eastern United States) may have a different canopy light environment compared to arid regions.

The following experiments were designed to determine the influence of the ambient light environment on nectar production, leaf gas exchange characteristics, and fruit physiology within apple canopies for humid conditions. Also, the use of instantaneous light measurements as estimates of cumulative seasonal light levels was tested by using inexpensive selective light sensors and programmable dataloggers to quantify ambient light levels at multiple positions within apple canopies throughout the growing season. Through these experiments, a better understanding will be gained about the interaction of the canopy light environment and the physiological processes within the canopy.

## LITERATURE REVIEW

Solar radiation provides energy for the growth and development of plants. The interaction of incident solar radiation with forest communities has been the focus of intensive research for nearly a century, and has been reviewed by Anderson (1964a) and Evans (1956). Research conducted with apples has been focused primarily on the influence of the light environment within the canopy on fruit production and quality, and the interaction of the light environment with climate, orchard design, pruning techniques, and management procedures. These data demonstrate that the light environment of an apple canopy influences leaf physiology, vegetative growth, flower bud formation, fruit set, fruit size and development, and fruit quality. However, the data suggest that the influence of light on fruit quality is often inconsistent, and varies with climatic conditions. This review concentrates on the measurement of light within plant communities and individual canopies, and the effect of light level on leaf physiology and fruit quality of apple.

*Definition of "light"*. Solar radiation is either transmitted, reflected, or absorbed by the atmosphere. The majority of the solar energy reaching the earth's surface is between 250 and 2000 nm, with a peak in the visible portion. "Light" has been used to describe different, yet related entities. In biological studies light has often been defined as a restricted waveband, 400-700 nm, termed photosynthetically active

radiation (PAR). This waveband is the principle portion of the spectrum responsible for photosynthesis. Light measurements are expressed in a variety of units, but where possible in this review, measurements will be converted to percent full sun (%FS) or quantum units of PAR ( $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) according to Thimijan and Heins (1983).

*Measurement techniques.* Measurement techniques for the characterization of the light environment within forest communities and individual plant canopies have been reviewed by Anderson (1964a) and Jackson (1980b). Solar radiation has been measured with illuminometers (Christopher, 1934), albedometers (Khromenko, 1972), pyranometers (Proctor et al., 1975; Vezina, 1961), and photochemical methods (Verheij and Verwer, 1973) for the past century in forest communities and plant canopies. Heinicke (1963a) used an integrative technique with a photosensitive uranyl oxalate solution to characterize the light environment of apple trees. Uranyl oxalate actinometers were placed throughout an apple canopy, and the quantification of light was based on the amount of photo-degradation of the solution from the light impinging on the solution container. Anderson (1964a) severely criticized the technique because the uranyl oxalate solutions are most sensitive to ultra violet and infrared radiation, and she questioned whether the measured radiation levels represented physiologically active radiation levels.

Photovoltaic cells (photocells) have been widely used in both forest communities and plant canopies in the past and at the present. Selenium and silicon photocell sensors are commercially available, and in combination with specific filters that exclude certain wavelengths, these instruments are extremely versatile. Inexpensive photocell sensors may be constructed which compare favorably to commercially available sensors (Grappadelli and Coston, 1988). One criticism of photocells, and in particular selenium photocells, is the instability of the electrical current generated by the photocell due to environmental changes and aging, resulting in measurement error. Also, photocells are generally small, allowing for the measurement of a limited area.

Most instruments measuring irradiance on a horizontal plane have some "cosine" error; that is, their response is proportional to the cosine of the angle of incidence of the incident radiation (Biggs et al., 1971). As such, significant measurement errors occur when rays of light approach a horizontal impact. The greatest concern is at low solar angles. Sensor design may influence the cosine response. Commercially produced photocell sensors and radiometers account for this error to some degree by using diffusive sensor heads with bevelled edges, which improve the cosine response. These sensors are termed "cosine corrected".

Photographic techniques have been used to quantify the light environment of forest communities (Anderson, 1964b), and apple canopies (Lakso, 1976; Lakso, 1980). In 'McIntosh' trees, fisheye photography correlated well with light (PAR)

levels measured with a quantum sensor (Lakso, 1976; Lakso, 1980), and this technique was useful for comparing light levels within 'Golden Delicious' canopies under different management systems (Ferree, 1989). The technique is fast and provides a permanent record of the light environment of the tree which can be correlated with specific biological responses. This technique is unable to account for leaf transmission, and may underestimate radiant energy levels in the near infrared. Measurements may be difficult to compare among climatic regions, such as predominantly clear climates, and predominantly overcast or cloudy climates (Lakso, 1980).

*Instantaneous and integrated measurements.* Instantaneous light measurements have often been used to characterize the light environment of plant canopies, with the relative light levels expressed as a percentage of full sun (%FS) (Marini and Barden, 1982a; Lakso, 1980). The validity or comparison of these instantaneous measurements with integrative light measurements has been questioned (Anderson, 1964a; Cain, 1973). Ambient light conditions change rapidly during the day due to environmental conditions (Anderson, 1964b) and solar angle, and it may be difficult to quantify the changing ambient light conditions during measurement. It has been proposed that meaningful instantaneous measurements can only be made under a constant ambient light environment such as a uniformly overcast day (Anderson, 1964b; Evans, 1956).

*Direct and diffuse radiant energy.* Solar energy is continually altered in intensity and composition due to environmental conditions and solar angle which change the relative amounts of direct and diffuse (sky) components. Direct radiant energy travels in a straight line from the point source (sun) to the receiving object (leaf or canopy). Diffuse radiant energy is reflected off clouds, and impurities, and may impinge upon an object from any direction. Direct radiant energy is greatest under clear conditions, often accounting for 90% of the total radiant energy (Heinicke, 1967). The relative percentage of diffuse radiant energy increases with increasing haze or clouds in the atmosphere, and under overcast conditions it may constitute 100% of the total radiant energy.

The interaction of climate and environmental conditions with the light environment of forest communities has been studied in detail (Anderson 1964b; Anderson, 1964c; Evans et al., 1960; Vezina, 1961), and thoroughly reviewed (Anderson, 1964a; Evans, 1956). On clear, relatively cloud-free days direct radiation, measured as sunflecks, accounted for 80% of the radiant energy reaching the floor of a tropical rain forest (Evans et al., 1960). On a given clear day direct radiation was the greatest contributor to the total radiant energy; however, under a temperate forest in southern England, diffuse radiation was the most significant contributor to the radiant energy over the growing season (Anderson, 1964c).

The relative importance of direct and diffuse radiation within plant canopies remains unclear and often debated, and probably varies with climate. Instantaneous

PAR measurements have often been made on uniformly overcast days, thereby measuring only diffuse radiation and avoiding the complication of sunflecks (Marini and Marini, 1983). According to Anderson (1964c) this measurement technique would be valid in climates where diffuse radiation is the major contributor to the available solar radiation. Various methods account for sunflecks within apple canopies, including the line quantum sensor (Barritt et al., 1987) and other modified sensors that measure both diffuse and direct radiation with increased surface area of measurement (Marini and Barden, 1982a). These methods may be particularly important in climates with predominantly clear conditions where sunflecks are a major contributor to total radiant energy within the canopy.

Lakso and Musselman (1976) demonstrated that on a clear day there was very little PAR at interior canopy positions of an apple tree when there were no sunflecks (direct radiant energy); these data confirmed an earlier report by Heinicke (1967). Under hazy conditions there was appreciably more PAR at these interior positions due to an increase in diffuse radiant energy, and greater transmission into the canopy. These data suggest that in arid climates with predominantly clear conditions during the growing season and greater total radiant energy, the interior canopy may actually receive less radiant energy than in humid climates with predominantly cloudy or hazy conditions and less total radiant energy.

***Spectral distribution within a plant canopy.*** Federer and Tanner (1966) characterized the spectral distribution of diffuse light under corn, sugar maple, oak, pine, and spruce canopies. Differences were reported among the plant species, but in general there was one energy maximum at 550 nm, a minimum at 670 nm, and another maximum in the near-infrared. Spectral distribution also varied with weather condition (clear or cloudy), with some interaction among the species considered. Spectral distribution of sunflecks in all species, even at the deepest canopy positions was similar to ambient solar radiation, and this was confirmed in apple canopies (Looney, 1968).

The near-infrared enhancement was measured within apple canopies (Proctor et al., 1975), with a greater enhancement at increased planting densities (Suckling et al., 1975). As discussed earlier, the use of uranyl oxalate solutions by Heinicke (1963a), and other measurement techniques sensitive to infrared radiation have been criticized due to their spectral response. Looney (1968) measured the enhancement of near-infrared light in the interior of apple canopies, but he drew conclusions similar to Heinicke (1963a) about the light zones of a large apple tree. Spectral changes occur as radiation penetrates a plant canopy, but the biological significance of these changes remain unclear.

***Orchard management systems and pruning.*** Available solar radiation is determined by latitude and climate (cloud cover). Orchard management schemes have been

devised to provide the most efficient use of this available energy. Row orientation interacts with the interception of solar radiation; Jackson and Palmer (1972) reported that East-West oriented rows were more subject to seasonal variation in the percent of intercepted radiation than North-South oriented rows, and the effect varied with latitude. The north side of East-West oriented rows was poorly illuminated compared to the south side, and the difference was accentuated at higher latitudes. The ratio of the in-row height to the row width also influenced light interception, with small increases in the in-row height resulting in large reductions in intercepted direct light by adjacent rows (Jackson and Palmer, 1972).

Regardless of the management system, larger trees have lower light transmission into the canopy (Heinicke, 1963b, 1964), and light levels decrease from the top to the bottom, and from the outside to the inside of the tree (Ferree, 1980). Integrated light measurements at the darkest canopy positions of four management systems demonstrated that light penetration into seven-year-old 'Golden Delicious' trees was greatest into trellis-trained trees, followed by slender spindle, interstem hedgerow, and pyramid hedgerow trees (Ferree and Hall, 1980; Ferree, 1989), and light levels were correlated with tree height. Slender spindle and trellis canopy light levels were most influenced by solar angle with greater light levels on the east quadrants in the morning and west quadrants in the afternoon.

Field experiments to determine the best combinations of tree size, shape, spacing, and pruning for optimization of light for yield and fruit quality may take

many years, with great land and labor expense. Another alternative is the use of computer modelling to simulate the light environment of different systems and management techniques with respect to latitude and climate. The light environment of different orchard designs has been modelled by Jackson (1980a), Jackson and Palmer (1972), and Palmer (1980), and reviewed by Jackson (1980b). The models used by these researchers are a simplification of reality, but they define the basic functional relationships. Limitations of these models include the inability to account for sunflecks, foliage distribution patterns of different cultivars, and training/pruning techniques.

Pruning technique interacts with the canopy light environment. Continued use of cutter-bar hedging on 10-ft high hedges of 'McIntosh' reduced production of fruiting spurs, and induced a dense outer periphery which increased shading and reduced bearing (Cain, 1971). Slotting-saw treatment to the hedgerow increased light penetration into the interior of the tree, and there was nearly 3 times as many new spurs and a 4-fold increase in flowering spurs. Summer pruning increased light penetration into the canopy of 'Starking Delicious', but in the year following treatment light penetration was greater into dormant pruned trees than summer pruned trees (Marini and Barden, 1982b).

*Leaf physiology and vegetative growth.* Net photosynthesis (Pn) of apple leaves, measured at saturating light levels, was reduced by growing trees in the shade

(Barden, 1974; Barden, 1977; Rom and Ferree, 1986) and by natural canopy shade (Heinicke, 1966a; Mika and Antoszewski, 1972; Khromenko, 1972; Seeley and Kammereck, 1977; Porpiglia and Barden, 1980). Pn of "shade" 'Delicious' leaves was about 70% that of "sun" leaves at saturating light levels (Barden, 1977). Mika and Antoszewski (1972) found the outer zone of 7-year-old 'Bancroft' and 'Jonathan' trees to have 650-830 W·m<sup>-2</sup> of total radiant energy (average instantaneous), while the interior positions had 80-150 W·m<sup>-2</sup>, and Pn of the outer canopy was 3 times higher than that of the interior canopy measured at ambient light levels. The mean Pn rate in the inner zone of 4-year-old 'Bancroft' trees trained to a compact crown was 2.5 times lower than the Pn rate in the inner zone of trees trained to an open canopy structure. Similar results were found by Heinicke (1966a) with 'Delicious', which had an outer zone receiving full sun, and an interior zone in the shade with a 29% lower Pn rate. Pn measurements in these studies were made on bright clear days, and direct light or sunflecks were important in determining the Pn rate. Dark respiration was reduced in 'Delicious' leaves by imposed shade treatments (Barden, 1974; Barden, 1977) and by natural canopy shading (Porpiglia and Barden, 1980). The adaptation of dark respiration to shading was faster than that of Pn. Transpiration was reduced by shading of 'Starkrimson' trees in the greenhouse (Rom and Ferree, 1986).

In apple, sorbitol is the major ethanol-soluble carbohydrate constituent of the leaves, a major storage carbohydrate for hexose sugars (Chong and Taper, 1971a),

and a major translocation carbohydrate (Webb and Burley, 1962). Sorbitol and starch concentrations in leaves decreased during darkness, with a rapid rise during daylight; sucrose, fructose, and glucose had more irregular patterns (Chong and Taper, 1971a). The greatest daily sorbitol concentrations measured during the growing season corresponded closely to the greatest solar radiation levels in mid-July (Chong and Taper, 1971b). These data suggest that interior canopy positions receiving less solar radiation could have lower sorbitol and carbohydrate levels, but in walnut there was no difference in carbohydrate content of leaves at interior and exterior locations (Ryugo et al., 1980).

Shading of 'Cox' trees increased the potassium and magnesium concentration (% dry weight) of leaves from the middle regions of extension shoots in the year of shading, but nitrogen, magnesium, and calcium concentrations were reduced in the year following shade removal (Jackson and Palmer, 1977a). Mineral weight per unit leaf area of nitrogen, calcium, magnesium, potassium, and phosphorous increased with increasing PAR within a prune canopy, but nutrient concentrations expressed as a percent dry weight were not influenced by PAR (Weinbaum et al., 1989). The influence of shading on both current and the following year's nutrient concentrations may influence fruit quality and storage.

Apple leaf morphology was influenced by shading, and may partially explain the influence of shade on leaf physiology. Barden (1977) found that specific leaf weight (SLW), or dry weight per unit area was suppressed by shade, both when shade

treatments were applied during leaf expansion and after the leaves were fully expanded. Shading of 'Cox' trees (11% FS) suppressed leaf thickness, dry weight per unit leaf area, and the thickness of the palisade layer (Jackson and Palmer, 1977a). Dry weight to fresh weight ratio was suppressed and individual leaf area enhanced by shade treatment. There was evidence of a residual effect of shade in the following year. Marini and Barden (1981) suggested that the effect of the light environment on leaf morphology allowed for the use of the leaf as an indirect measure of the previous, and present light environment.

Shoot-length and dry weight increase were suppressed by 10% and 50%, respectively, by shading (20% FS) container-grown 'Delicious' trees, but leaf area was unaffected (Barden, 1977). Shading (11% FS) of 'Cox' trees for 1 year suppressed the number and weight of new shoots, the fresh weight per unit length of shoot, and trunk girth increment; two years of shade had a greater effect (Jackson and Palmer, 1977a). The year following shade removal, the previously-shaded trees produced fewer new shoots than unshaded control trees.

*Flower bud formation and fruit set.* 'Cox' trees shaded for the entire 1970 growing season had fewer flower clusters than unshaded control trees in the spring of 1971 (Jackson and Palmer, 1977b). The effect was progressively more severe with increasing shade level, with an 82% reduction in flowering clusters at 11% FS. Fruitlet retention (number of fruit per 100 flowering clusters) was reduced by 32%

with the 11% FS shade treatment in the year of shading, and 25% in the following year after shade removal (Jackson and Palmer, 1977b). Moderate shade treatments of 37 and 25% FS also reduced fruitlet retention, but the effect was less severe. With 'Delicious', early-season shading (16% FS) from budbreak to 34 days after petal fall (Rom and Ferree, 1984), and shading for the entire season (80% FS) (Doud and Ferree, 1980) reduced fruitlet retention. Reduced carbohydrate levels and altered hormone levels probably were responsible for the reduced flowering and fruitlet retention in the previous studies. Imposed shade treatments have been proposed as a possible technique for post-bloom thinning of apples (Byers et al., 1985; Byers et al., 1990a; Byers et al., 1990b).

#### **FRUIT QUALITY:**

***Soluble solids.*** The soluble solids content (SSC) of 'Delicious' fruit was reduced 14% following shading of whole trees (80% FS) for the entire season (Doud and Ferree, 1980). SSC was correlated with the degree of shading in 'Delicious' limbs shaded from about 50 DAFB until harvest (Seeley et al., 1980; Robinson et al., 1983). Reductions in SSC were greater than reductions in red color at the same light level, indicating that light levels adequate for red color development may not result in adequate SSC levels; particularly in the high-coloring 'Delicious' strains. Rom and Ferree (1984) reported that severe shading (16% FS) from bud-break to fruit-set had

no effect on SSC at harvest on greenhouse-grown 'Delicious' trees, indicating that timing of the shade treatment was also important.

Imposed shade treatments do not mimic the natural shade within a canopy because these treatments are continuous, exclude sunflecks, and influence all leaves, including both the highly productive sun leaves and the less productive shade leaves. Besides the effect of lower light levels on existing fully-expanded leaves, the leaves unfolding under the imposed shade would be morphologically altered, and have less Pn potential (Barden, 1977; Jackson and Palmer, 1977a). Magness (1928a) reported that SSC of apple fruit was reduced following removal of substantial leaf area on girdled limbs, demonstrating the importance of leaves for adequate SSC. The imposed shade treatments probably influenced fruit SSC by reducing the amount of carbohydrates available to the fruit due to reduced whole-tree Pn.

In a natural apple canopy, Heinicke (1966a) found an 8% and 11% reduction in SSC for 'Delicious' and 'McIntosh', respectively, developing in 20% FS compared to FS. Barritt et al. (1987) found a 5% reduction in SSC of fruit from the top to the bottom of 'Delicious' trees. Light level explained about 50% of the variation in SSC. Similar reductions in SSC were found with 'Golden Delicious' (Ferree, 1989). Some of the other factors that could contribute to SSC variation are the number of leaves in the vicinity of the fruit, leaf efficiency, and spur age. Shading may also reduce fruit SSC by direct shading of the fruit, as reported for 'McIntosh' (Proctor and Loughheed, 1976).

**Fruit size.** Small 'Cox' trees were shaded to 37, 25, or 11% FS during the post-bloom growing season, with all levels reducing fruit weight or size by up to 66% at the greatest shade level (Jackson and Palmer, 1977b). The reduction in fruit size was caused by reductions in cell size, and the number of cells per fruit (Jackson et al., 1977). Seeley et al. (1980) and Robinson et al. (1983) reported reduced fruit size on shaded 'Delicious' limbs. Shade levels ranged from 1 to 100% FS from 45 days after full bloom until harvest. Light explained 75% and 45% of the variation in fruit size in the two experiments, respectively, but this was improved to 85% by Seeley et al. (1980) by using data from 1 tree only. The reduction in cell numbers indicates that shading early in the season may be critical for determining ultimate fruit size at harvest. Under greenhouse conditions; however, Rom and Ferree (1984) found no effect of shading from budbreak to fruit set. Ambient light levels were only 35% FS, or 65% FS with artificial lighting, and may have masked any effect of shading on fruit size.

'Delicious' and 'McIntosh' fruit from canopy positions receiving greater than 50% FS were 15% and 27% larger, respectively, than fruit receiving 20% FS (Heinicke, 1966b). Fruit size was greatest at the more-exposed peripheral canopy positions of 'Cox' trees from 3 different management systems (Jackson, 1967; Jackson, 1970). Position of the fruit on the tree explained about 40% of the variation in fruit size, and light level was proposed as the cause. Age of the fruiting wood accounted for about 10% of the variation in size. Barritt et al. (1987)

measured a 31% decrease in 'Delicious' fruit size from the top to the bottom of the canopy of the tree. These canopy positions corresponded to 48, 23, and 9% FS, respectively. Canopy light level explained about 12% of the variation in fruit size, indicating that other unexplained factors were important for fruit size.

***Fruit shape.*** Webster and Crowe (1971) reported that full shade (lath-type wooden cover blocked all direct light, but open on north side and bottom) applied early in the season, and for the entire season increased the length/diameter (L/D) ratio of 'McIntosh' compared to unshaded controls. Similarly, an increase in the L/D ratio was found in 'Starkrimson Delicious' from young greenhouse-grown trees receiving 16% FS from budbreak to fruit set (Rom and Ferree, 1984). The increase in L/D ratio with shading can be explained by an influence on cell division and expansion within the fruit (Jackson et al., 1977). Seeley et al. (1980) found a small (1%) increase in the L/D ratio of 'Miller Sturdeespur Delicious' as available light increased from 5 to 100% FS. There is little evidence for an effect of natural canopy shading on L/D ratio.

***Anthocyanin formation and the development of red color.*** The formation of red color in apples depends on the synthesis of anthocyanin in the apple skin. Pearce and Streeter (1931) reported that the wavelengths between 360 and 450 nm were optimal for red color development in 'McIntosh'. Siegelman and Hendricks (1958) found

peak red color development of 'Jonathan' at 650 nm, with a subsidiary peak at 600 nm. The authors gave no explanation for the differing results from Pearce and Streeter (1931), but the use of different filters may have been the reason.

Siegelman and Hendricks (1958) demonstrated a two-stage synthesis of anthocyanin in excised 'Jonathan' slices following continuous illumination with fluorescent light. A 20-hour induction period with no anthocyanin formation was followed by a period of linear anthocyanin formation. The amount of anthocyanin formed after 84 hrs of illumination was linearly related to irradiance level from 270 to 1000 ft-c (40 to 150  $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ), the greatest irradiance level tested. A minimum irradiance level of 100 ft-c for 84 hr (4.5  $\text{moles} \cdot \text{m}^{-2}$ ) was required for anthocyanin synthesis. Proctor and Creasy (1971) measured induction of anthocyanin synthesis in attached 'McIntosh' fruit 12-15 hours after supplemental irradiation with fluorescent lighting; a minimum irradiance level of 5  $\text{W} \cdot \text{m}^{-2}$  (23  $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) was necessary to induce synthesis. There was also a linear increase in anthocyanin production up to 83  $\mu\text{moles} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ , which was the greatest irradiance level tested. Proctor and Loughheed (1976) reported superior anthocyanin production in 'Golden Delicious', 'Mutsu', and 'McIntosh' when fruit were covered about a month after bloom and then exposed 20 to 30 days before harvest compared to control fruit which were not covered. Covering and subsequent exposure of fruit resulted in superior red color development when compared to supplemental irradiation, and timing of the exposure of the fruit influenced the amount of anthocyanin formed. A period of

darkness or reduced light levels previous to illumination also enhanced anthocyanin synthesis in 'Jonathan' (Siegelman and Hendricks, 1958) and 'Delicious' (Doud and Ferree, 1980).

Cool nights (13C) and warm days (25C) resulted in optimal red color development in 'McIntosh' fruit receiving adequate light levels for color formation (Creasy, 1968). Temperature influences anthocyanin synthesis at a given irradiance level by altering levels of a key enzyme in anthocyanin synthesis, phenylalanine ammonia-lyase (PAL). PAL levels were greater at low temperatures (12C) compared to high temperatures (30C) in unripe 'Jonathan' fruit (measured by ethylene concentration), and were greater in ripe than unripe fruit (Faragher, 1983). Apple fruit with greater SSC had superior color compared to fruit lower in SSC (Magness, 1928b). Fletcher (1929) demonstrated the positive effect of light on red color development in a range of apple cultivars, and the enhancement of this effect with soil applications of glucose, which increased the SSC of the fruit. These studies illustrate the need for a balance between sufficient leaf area for sugar production, and adequate light levels for color development.

Shading of individual fruits within the canopy reduced red color development in a range of apple cultivars (Schrader and Marth, 1931). Seeley et al. (1980) reported reduced red color of 'Miller Sturdeespur Delicious' on individual shaded limbs. An irradiance threshold of  $5 \text{ J} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  ( $23 \mu\text{moles} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) was reported below which no persistent color formation occurred, which agreed with Proctor and

Creasy (1971). In a similar study where 'Miller Sturdeespur Delicious' limbs were shaded to 5% FS, red color was unaffected (Robinson et al., 1983). The 5% FS irradiance level under the shade was still sufficient for adequate coloring of this high-coloring 'Delicious' strain.

With natural canopy shading, Heinicke (1966b) reported that color formation in 'Turner Delicious' and 'McIntosh' was closely related to light level in the vicinity of the fruit. The best color occurred when fruit were exposed to greater than 70% FS, with adequate red color development between 40% and 70% FS and inadequate color development when exposed to less than 40% FS. Barritt et al. (1987) found no consistent effect of natural canopy shading on red color development of 'Oregon Spur Delicious'.

***Mineral composition, ripening, and storage.*** Concentrations (fresh weight basis) of nitrogen, phosphorous, potassium, calcium, and magnesium did not differ in 'Cox' fruits of similar size from shaded (11% FS) or non-shaded conditions, but smaller fruit from the shaded conditions had higher concentrations of nitrogen, phosphorous, and calcium (Perring and Jackson, 1975; Jackson et al., 1977). 'Cox' fruits from trees shaded for one year developed less bitter pit, senescent breakdown, russet, and soft rots, and had increased shrivelling compared to fruit from non-shaded trees (Jackson et al., 1977). The year following shade removal there was a reversal in the trend,

with more bitter pit, senescent breakdown, russet, and soft rot. The difference can probably be explained by fruit size, calcium concentration, and crop load.

Shaded fruits are not simply physiologically retarded versions of unshaded fruits. Shaded 'Cox' fruits had less starch, both in absolute amount and as a percentage of dry matter than unshaded controls at the same date (Jackson et al, 1977). Onset of the climacteric rise in carbon dioxide was not influenced greatly by shading, although respiration rate per unit fresh weight was lower in shaded compared to unshaded fruit. However, Farhoomand et al. (1977) reported that the ripening pattern of 'Delicious' was hormonally controlled and progressed acropetally from the base to the end of the scaffold branches. Small, green interior fruit had greater ethylene concentrations than more exposed redder fruit, and were physiologically more advanced.

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## Chapter I

### **Canopy Position, Defoliation, and Girdling Influence Apple Nectar Production**

*Abstract.* Flowering spurs located at interior and exterior canopy positions of 'Stayman' and 'Delicious' apple (*Malus domestica* Borkh.) trees were girdled and/or defoliated to determine the influence on nectar production and composition. Nectar volume was less at exterior than at interior canopy positions of 'Delicious', but not for 'Stayman'. Girdling suppressed nectar production by 92%, and reduced the sugar concentration of the remaining nectar. Defoliation of nongirdled spurs had no effect on nectar sugar concentration, but defoliation of girdled spurs reduced nectar sugar concentration by 24%. Relative percentages of sucrose, glucose, and fructose, and the sucrose/hexose ratio were unaffected by any treatment. Nectar production of nongirdled spurs was not dependent on the presence of spur leaves.

## **Introduction**

The shaded interior canopy of apple trees is generally less productive than the better-exposed outer canopy. The difference in productivity has been attributed in part to a reduction in flower bud formation (Jackson and Palmer, 1977) and fruitlet retention (Byers et al., 1990) due to reduced light levels and a subsequent reduction in assimilated carbohydrates available to the developing fruit. Nectar production and carbohydrate composition could also be influenced by carbohydrate availability within the canopy (Wykes, 1952), thereby influencing honeybee foraging behavior (Waller, 1972; Wykes, 1952). Thus, pollination, and fruitlet retention within the canopy may be affected. The objective of this study was to evaluate the influence of canopy position, defoliation and girdling of flowering spurs on apple nectar production and composition.

## **Materials and Methods**

All trees were located at the Virginia Polytechnic Institute and State University Horticulture farm, Blacksburg, VA. Five 23-year-old 'Stayman'/MM.111 trees were used in 1989 with a 2x2 factorial arrangement of interior/exterior canopy positions and foliated/defoliated flowering spurs in a randomized complete block design (block = tree). In 1990, five 15-year-old 'Red Prince Delicious'/MM.111 trees were used with a 2x2x2 factorial arrangement of interior/exterior positions, foliated/defoliated, and girdled/nongirdled flowering spurs. A single unbranched

spur per treatment combination was selected within each tree based on uniformity of bud diameter and developmental stage. Individual spurs were defoliated and/or girdled at the tight cluster floral developmental stage and nectar samples were collected at full bloom (5 to 7 days later). Flowering spurs were covered with muslin bags 1 day before nectar collection to prevent honeybee visitation. Samples for sugar analysis were collected between 1100 and 1300 hr during periods of warm ( $>20^{\circ}\text{C}$ ), sunny weather by inserting a 1  $\mu\text{liter}$  microcapillary pipette into the nectary of a single flower (king bloom) and allowing the pipette to fill by capillary action. A single-flower sample was collected for sugar analysis for each treatment combination per tree.

Nectar volume was determined by measuring the portion of the 1  $\mu\text{liter}$  pipette(s) filled with nectar. Samples were expelled into microcentrifuge tubes containing 200  $\mu\text{liter}$  of 70% (v/v) ethanol, and stored at  $-22^{\circ}\text{C}$  until analysis. Qualitative and quantitative sugar analyses were performed with high-performance thin-layer chromatography (HPTLC) as described by Fell (1990) and modified by Campbell et al. (1990). Sucrose, glucose, and fructose levels were characterized because these are the predominant sugars found in apple nectar (Baker and Baker, 1983; Wykes, 1952). Sorbitol, the major translocated carbohydrate in apple, was not found among a range of apple cultivar nectars in a previous study (Campbell et al., 1990).

Data were tested by analysis of variance and significance levels for the main effects and interactions are presented in Table 1 (only significant interactions). Where there was a significant interaction ( $P > F = 0.05$ ), means were separated by Tukey's HSD.

### Results and Discussion

Nectar volume (1.7 to 1.8  $\mu\text{l}$ ), sucrose (55-56%), glucose (19-20%), and fructose (25%) percentages, and sucrose/hexose ratio (1.2-1.3) were unaffected by either canopy position or defoliation of individual 'Stayman' spurs in 1989 (data not shown). Nectar sugar concentration was 10% higher in defoliated than in foliated spurs. There was no interaction between canopy position and foliation treatments. Sucrose (41-48%), glucose (25-30%), and fructose (25-33%) percentages, and sucrose/hexose ratio (0.7-0.9) of 'Delicious' nectar (1990) were unaffected by canopy position, girdling, or defoliation of individual spurs (data not shown). Nectar volume was 29% greater at interior canopy positions than exterior positions, and there was a trend ( $P > F = 0.15$ ) for greater sugar concentration at the exterior positions (Table 1). Girdling spurs lowered nectar volume by 92%. With nongirdled spurs, defoliation had no effect on nectar sugar concentration, but with girdled spurs, defoliation lowered sugar concentration by 24%.

The nectar sugar concentration of nongirdled spurs ranged from 500 to 600  $\mu\text{g}\mu\text{liter}^{-1}$  (50 to 60% total sugar), as previously reported for apple nectar (Vansell,

Table 1. The influence of canopy position, defoliation, and girdling on 'Delicious' nectar production and composition in 1990.

Treatment			Nectar production	
Position	Foliation	Girdle	Nectar volume ( $\mu$ liter)	Sugar concentration ( $\mu$ g $\cdot\mu$ liter)
Interior	Defoliated	No	1.39 <sup>z</sup>	572 a
Exterior		No	1.06	596 a
Interior	Foliated	No	1.28	574 a
Exterior		No	1.05	606 a
Interior	Defoliated	Yes	0.12	418 c
Exterior		Yes	0.07	428 c
Interior	Foliated	Yes	0.15	524 b
Exterior		Yes	0.09	592 a
Significance ( $P > F$ ) <sup>y</sup>				
Foliation (F)			0.562	0.036
Girdle (G)			0.001	0.012
F x G			0.244	0.037
Position			0.025	0.150

<sup>z</sup> Data shown are the mean of 5 observations.

<sup>y</sup> Nonsignificant ( $P > F = 0.05$ ) interactions are not presented. If interaction significant, mean separation by Tukey's HSD.

1934; Wykes, 1952). 'Stayman' and 'Delicious' nectar composition were within the range previously reported for apple cultivar nectars (Campbell et al., 1990). Greater evaporation at the exterior positions of 'Delicious' may have caused the reduction in nectar volume, which is supported by the trend for increased sugar concentrations at these positions. Vansell (1934) reported that plum nectar volume and sugar concentration varied greatly during the day due to changing relative humidity, temperature, and wind speed. Nectar volume was unaffected by canopy position in 'Stayman', however, indicating a difference between cultivars or years. Honeybee visitation was not evaluated in our study, but based on previous studies (Waller, 1972; Wykes, 1952) we doubt that the differences in nectar production and composition measured in our study would influence honeybee foraging behavior within the canopy.

Wykes (1952) reported that girdling and defoliation treatments, applied both alone and in combination to flowering shoots of horse chestnut (*Aesculus hippocastanum* L.), reduced nectar volume, with cessation of nectar production 11 days after girdling and defoliation. In our study girdling alone also resulted in almost complete cessation of nectar production 7 days after treatment, but defoliation of individual spurs alone had no effect. Girdled and defoliated flowering shoots of horse chestnut had a 38% lower nectar sugar concentration than the control shoots 5 days after treatment (Wykes, 1952), a result similar to ours with apple. However,

in contrast to our results, defoliation of nongirdled horse chestnut shoots also reduced nectar sugar concentration (24%).

Horse chestnut trees bloom later in the spring than apple and have a large, fully-expanded leaf area present at flowering; apple trees have sparse foliage present at flowering. Thus, reserve carbohydrate levels at the time of flowering could be quite different in these 2 species, possibly influencing the effect of defoliation of spurs or individual shoots on nectar production. Therefore, unlike chestnut, nectar production in apple is not dependent on the presence of spur leaves, but rather on translocated materials from other sources.

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## Chapter II

### Canopy Position Affects Light Response Curves for Gas Exchange Characteristics of Apple Spur Leaves

*Abstract.* Light response curves for gas exchange characteristics were developed for 'Stayman' and 'Delicious' spur leaves from interior, intermediate, and exterior canopy positions throughout the season. At full bloom (FB), before the leaves were fully-expanded, exterior leaves had greater maximum rates of net photosynthesis ( $P_n$ ), and a distinct  $P_n$  light response curve compared to the interior leaves. Intermediate leaves had intermediate  $P_n$  rates and light response curves.  $P_n$  light response curves for all three 'Delicious' canopy positions were distinct from FB + 6 weeks until the end of the season. Interior leaves had maximum  $P_n$  rates of only 50-60% of those for the exterior leaves from FB + 10 weeks until the end of the season. Light saturation levels were greater for the exterior leaves compared to the interior or intermediate leaves. Exterior leaves had a tendency throughout the season for greater quantum efficiency of  $P_n$  at sub-saturating light levels compared to interior or intermediate leaves. Stomatal conductance was greater for the exterior compared to the interior or intermediate leaves of 'Delicious' on all dates. Water use efficiency was equivalent among leaves for all three positions. Exterior leaves had greater specific leaf weight, dark respiration, and incident light levels on all dates compared to the interior or intermediate leaves.

## Introduction

Light environment influences leaf anatomy, morphology and physiology among a wide range of plant species (Bazzaz and Carlson, 1982; Fails et al., 1982a; Fails et al., 1982b; Mahall and Schlesinger, 1982; Syvertson, 1984). Consequently, natural shading within a plant canopy results in anatomically distinct leaves with differing gas exchange characteristics (Nobel, 1976; Schaffer and Gaye, 1989). Previous studies with apple have focused primarily on the influence of the light environment on maximum photosynthetic rates either under light-saturated conditions (Barden, 1974; 1977; Porpiglia and Barden, 1980), or ambient light conditions (Heinicke, 1966). However, because light levels within the majority of an apple canopy are below light saturation (Heinicke, 1963; Porpiglia and Barden, 1980), gas exchange responses to differing light levels (light response curves) are of interest. Also, there is little information available on how light response curves for gas exchange characteristics change during the season for leaves at different canopy positions. Such information could influence pruning practices, and could be useful for modelling whole-canopy gas exchange characteristics. The objectives of this study were to develop light response curves for the gas exchange characteristics of apple spur leaves from interior, intermediate, and exterior canopy positions, and to determine how these relationships change over time.

## Material and Methods

All trees were located on the Virginia Polytechnic Institute and State Univ. Horticulture Farm, Blacksburg, VA. Five 23-year-old 'Stayman'/MM.111 were used in 1989, and four 15-year-old 'Red Prince Delicious'/MM.111 were used in 1990. 'Stayman' trees had an average height and width of 6.1 and 5.1 m, respectively, and an average trunk circumference of 79 cm. Rows were oriented in a N-S direction with a 6.1 m in-row spacing, and 6.1 m between-row spacing. 'Delicious' trees had an average height and width of 5.4 and 4.8 m, respectively, and a trunk circumference of 60 cm. Rows were oriented in an E-W direction with a 5.5 m in-row spacing, and a 6.1 m between-row spacing. At bud-break, four nonfruiting spurs in 1989, and 8 nonfruiting spurs in 1990 were tagged at each of the interior, intermediate, and exterior canopy positions of each tree; one spur was randomly selected at each position per tree per measurement date. Exterior spurs were selected on second-year wood as near to the periphery of the canopy as possible, intermediate spurs were selected about 40 to 60 cm towards the trunk from the exterior position, and interior spurs were selected within 30 cm of the trunk. All spurs were selected on the west side of the 'Stayman' trees and the south side of the 'Delicious' trees, and were chosen for uniformity of bud diameter and stage of development.

Light response curves were developed for 'Stayman' in 1989 on 4 dates: full bloom (FB), and FB + 2, 4, and 18 weeks, and for 'Delicious' in 1990 on 8 dates: FB, and FB + 2, 4, 6, 10, 14, 18, and 22 weeks. Gas exchange characteristics were

measured on one leaf per spur per canopy position per tree. On the day before measurement, spurs were detached from the trees between 1800 and 2000 hr and the cut ends were placed in water overnight in the laboratory. Net photosynthesis (Pn) was measured in an open system with an Anarad model AR-600 infrared gas analyzer (Anarad, Santa Barbara, CA). The leaf chamber was a modification of the chamber described by Syvertson and Smith (1983), but without a heat exchanger. Fans were used to negate boundary layer resistance. Air flow through the chamber was maintained at 0.033 or 0.05 liter·sec<sup>-1</sup>, depending on leaf area. Air temperature within the chamber was maintained at 28 ± 3C. Lighting was provided by 500R/3FL lamps (Westinghouse), and light levels were altered by covering the chambers with layers of neutral screening. Shading treatments were applied from least to most shade without randomization, as a preliminary experiment yielded equal results for randomized and nonrandomized shading treatments. Photosynthetic photon flux density (PPFD) was measured at each shade level in the laboratory with a quantum sensor at the level of the leaf. Following Pn measurements in the light, dark respiration was measured by turning off the lights and covering the chambers for 15 min. Pn was the only gas exchange characteristic measured for 'Stayman' leaves.

For 'Delicious' leaves dew point of the air in the chamber was measured simultaneously with Pn with a General Eastern model 1100 dew point hygrometer (General Eastern Instruments, Watertown, Mass.). These measurements were used to calculate stomatal conductance ( $g_s$ ) according to Moon and Flore (1986).

Intercellular CO<sub>2</sub> concentrations could not be calculated because absolute concentration of CO<sub>2</sub> in the chamber was not recorded. Water use efficiency (WUE) was calculated by dividing P<sub>n</sub> by transpiration (from dew point measurements). Following gas-exchange measurements, the leaves were removed and area measured with a LI-3000 leaf area meter (Li-COR, Lincoln, Neb.). Leaves were dried at 60C for 3 days, weighed, and specific leaf weight (SLW) was calculated. Photosynthetic photon flux density (PPFD) was measured at each spur position within the 'Delicious' canopy with a LI-COR quantum sensor (Model LI-185, Li-COR, Lincoln, NB) on the first overcast day following gas exchange measurements, and expressed as a percentage of incident PPFD (%IPPFD).

Light response curves for P<sub>n</sub> were fit to the data by two parameter nonlinear regression analysis using the proc NLIN procedure in SAS (SAS, 1985). These regression models are based on MacArthur-Wilson equilibrium equations developed to model zoological colonization on noninteractive islands (MacArthur and Wilson, 1963) given here as:

$$P_n = S_{p_n} * (1 - e^{-G * PPFD})$$

where S<sub>p<sub>n</sub></sub> is the equilibrium or maximum P<sub>n</sub> rate, and G is the rate of approach to equilibrium. Light response curves for g<sub>s</sub> were fit to the data using three parameter nonlinear regression because g<sub>s</sub> data did not approach 0 at 0 PPFD, making the two

parameter nonlinear model statistically inferior for these data. The three parameter equation is:

$$g_s = S_{gs} - (R * e^{-G * PPFDD})$$

where  $S_{gs}$  is the equilibrium or maximum  $g_s$  rate,  $G$  is the rate of approach to equilibrium, and  $R$  is the  $S_{gs}$  - (y-axis intercept). Indicator (dummy) variables were used to test all pairwise comparisons of regression models per date per year (Montgomery and Peck, 1982). Experimentwise error rates were held constant at  $\alpha=0.05$  by adjusting the alpha level for each comparison ( $\alpha$ /number of pairwise comparisons). Pseudo  $R^2$  were used to assess goodness-of-fit and were determined for each model by dividing the regression sums of squares by the total uncorrected sums of squares. PPFDD level for 95% saturation of  $P_n$  (light saturation point) was calculated for each position and date using the two equations above, but were not statistically compared.

## Results

Differences in the  $P_n$  light response curves occurred at FB for spur leaves from the three 'Stayman' canopy positions (Table 1). The exterior leaves had a greater equilibrium  $P_n$  level ( $S_{P_n}$ ) than the interior leaves; intermediate leaves had an intermediate  $S_{P_n}$ . On the remaining dates, FB + 2, 4, and 18 weeks, the exterior

Table 1. Regression coefficients for net photosynthetic ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) light response curves, and light saturation levels of 'Stayman' leaves from interior, intermediate, and exterior canopy positions at 4 sampling dates.<sup>2</sup> Equation:  $P_n = S_{P_n} * (1 - e^{-(G * \text{PPFD})})$ .

Canopy position	Regression coefficients ( $P_n$ )		Light saturation level <sup>y</sup>
	$S_{P_n}$	G	
		<i>FB</i>	
Interior	4.5 a	0.0042 a	713
Intermediate	6.5 ab	0.0040 a	748
Exterior	7.8 b	0.0033 a	908
		<i>FB + 2 weeks</i>	
Interior	14.2 a	0.0040 b	748
Intermediate	16.2 a	0.0039 b	768
Exterior	21.7 b	0.0032 a	936
		<i>FB + 4 weeks</i>	
Interior	15.5 a	0.0064 b	468
Intermediate	15.5 a	0.0056 b	534
Exterior	18.3 b	0.0037 a	810
		<i>FB + 18 weeks</i>	
Interior	8.6 a	0.0073 b	410
Intermediate	9.6 a	0.0061 b	491
Exterior	13.0 b	0.0040 a	748

<sup>2</sup> Coefficients within columns and dates followed by the same letter do not differ at an experimentwise error rate of 0.05 ( $n = 30$ ). Coefficients were compared with indicator variables.

<sup>y</sup> PPFD level ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) where  $P_n$  was 95% of maximum.

leaves had a greater  $S_{P_n}$  and rate of approach to equilibrium (indicated by a lower  $G$ ), and the interior and intermediate leaves had equivalent saturation curves. Similar results were found for 'Delicious' in 1990, but the increased frequency of measurement better illustrated seasonal trends. Again, at FB there were differences in the  $P_n$  light response curves of spur leaves from the 3 canopy positions (Table 2 and Fig. 1). The exterior leaves had a greater  $S_{P_n}$  and lower  $G$  than the interior leaves. The intermediate leaves had intermediate  $S_{P_n}$  and  $G$  values. By FB + 2, and 4 weeks both the interior and intermediate leaves had smaller  $S_{P_n}$  values than the exterior leaves, and interior and exterior leaves still differed in  $G$ . By FB + 6 weeks, and for the remainder of the season (FB + 10, 14, 18, 22 weeks) leaves from all three positions differed in  $S_{P_n}$ . Interior and exterior leaves also had different  $G$  values, but  $G$  values were equal for the interior and intermediate leaves. Pseudo  $R^2$  were  $\geq 0.95$  for all regression curves, demonstrating the excellent goodness-of-fit for the models to the data, as seen in Fig. 1.

Light saturation points for  $P_n$  were greater for the exterior leaves of both 'Stayman' and 'Delicious' on all dates (Table 1 and 2), as seen graphically for 'Delicious' (Fig. 1). Minimum light saturation points for leaves at all positions were reached by FB + 14, or 18 weeks with 'Delicious'. Exterior leaves appeared to have greater quantum efficiency at sub-saturating PPFD levels than leaves at the other positions (Fig. 1), but when linear equations were fit to the  $P_n$  data at PPFD

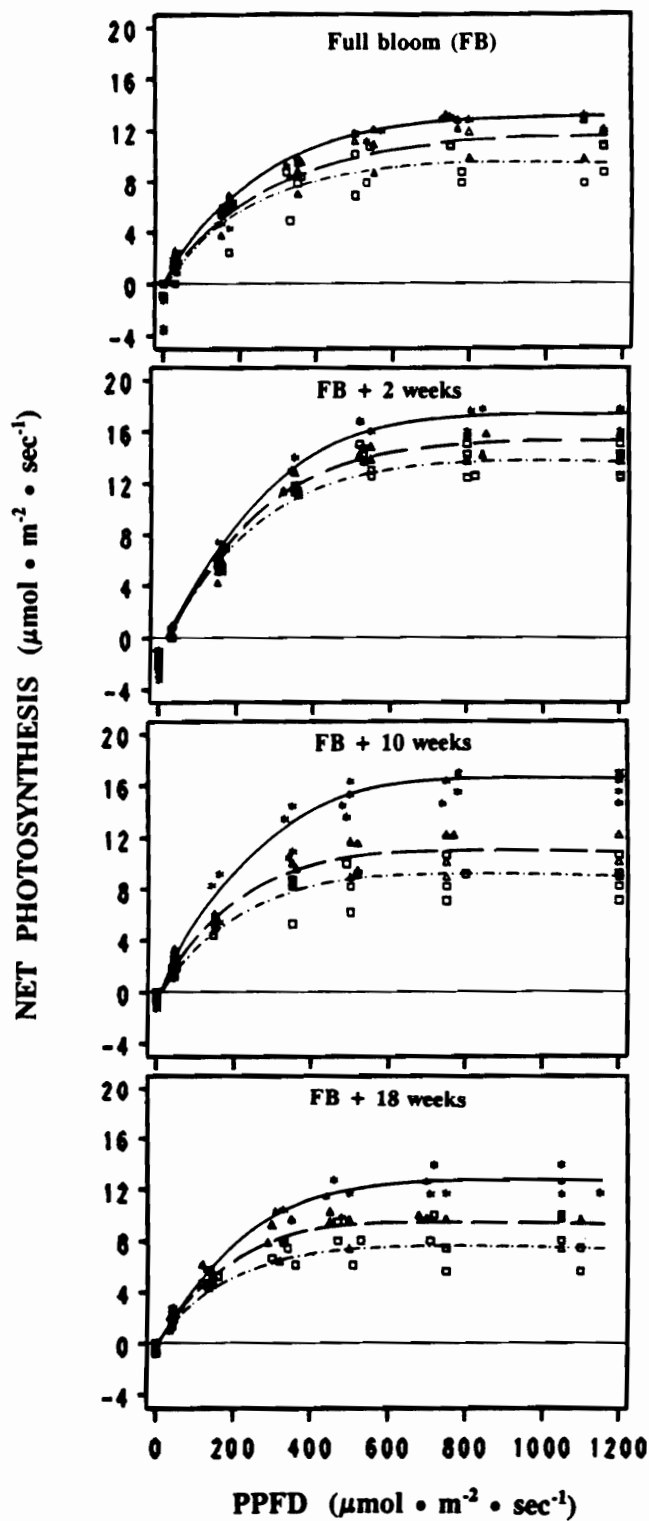
Table 2. Regression coefficients for light response curves of net photosynthesis ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) and stomatal conductance ( $\text{mmol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ), and light saturation levels of 'Delicious' leaves from interior, intermediate and exterior canopy positions on 8 sampling dates.<sup>z</sup> Equations:  $P_n = S_{P_n} * (1 - e^{-(G * \text{PPFD})})$ ;  $g_s = S_g - (R - e^{-(G * \text{PPFD})})$ .

Canopy position	Coefficients (Pn)			Coefficients (g <sub>s</sub> )		
	S <sub>Pn</sub>	G	Light saturation level <sup>y</sup>	S <sub>g</sub>	G	R
<i>Full bloom (FB)</i>						
Interior	9.7 a	0.0045 b	666	88 a	0.0032 a	49 a
Intermediate	11.9 ab	0.0041 ab	730	103 ab	0.0050 a	59 a
Exterior	13.7 b	0.0032 a	936	133 b	0.0025 a	76 a
<i>FB + 2 weeks</i>						
Interior	14.3 a	0.0040 b	745	110 a	0.0043 a	62 a
Intermediate	15.4 a	0.0036 ab	832	137 ab	0.0020 a	85 a
Exterior	17.8 b	0.0034 a	881	150 b	0.0035 a	74 a
<i>FB + 4 weeks</i>						
Interior	12.4 a	0.0040 b	749	111 a	0.0020 a	82 a
Intermediate	13.2 a	0.0040 ab	749	139 ab	0.0030 a	74 a
Exterior	17.6 b	0.0035 a	856	180 b	0.0022 a	110 a
<i>FB + 6 weeks</i>						
Interior	13.3 a	0.0044 b	499	148 a	0.0038 a	81 a
Intermediate	14.6 b	0.0043 b	697	189 b	0.0024 a	122 a
Exterior	19.0 c	0.0034 a	881	194 b	0.0023 a	132 a
<i>FB + 10 weeks</i>						
Interior	8.8 a	0.0060 b	499	58 a	0.0150 a	30 a
Intermediate	11.1 b	0.0049 b	611	96 b	0.0100 a	50 a
Exterior	16.4 c	0.0040 a	750	112 b	0.0046 a	62 a
<i>FB + 14 weeks</i>						
Interior	6.7 a	0.0071 b	422	60 a	0.0088 a	22 a
Intermediate	8.2 b	0.0057 b	526	91 b	0.0031 a	34 a
Exterior	12.5 c	0.0041 a	731	103 b	0.0042 a	58 a
<i>FB + 18 weeks</i>						
Interior	7.9 a	0.0070 b	427	64 a	0.0052 a	24 a
Intermediate	9.4 b	0.0064 b	468	90 b	0.0064 a	32 a
Exterior	12.9 c	0.0041 a	731	98 b	0.0046 a	31 a
<i>FB + 22 weeks</i>						
Interior	7.1 a	0.0054 b	554	70 a	0.0011 a	40 a
Intermediate	9.3 b	0.0052 b	576	97 b	0.0020 a	38 a
Exterior	11.9 c	0.0039 a	768	109 b	0.0042 a	42 a

<sup>z</sup> Coefficients within columns and dates followed by the same letter do not differ at an experimentwise error rate of 0.05 (n = 24). Coefficients were compared with indicator variables.

<sup>y</sup> PPFD level ( $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$ ) where Pn was 95% of maximum.

Fig. 1. Light response curves of 'Delicious' spur leaves for net photosynthesis measured at full bloom (FB), FB + 2 weeks, FB + 10 weeks, and FB + 18 weeks. MacArthur-Wilson saturation equations represent the interior ( $\square$ , - · - · -), intermediate ( $\Delta$ , ---), and exterior (\*, —) canopy positions. See Table 2 for equations and coefficients.



levels below  $200 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  for each position and compared with indicator variables no statistical differences were found.

Exterior leaves had greater equilibrium  $g_s$  values ( $S_{gs}$ ) than interior leaves at FB + 0, 2, and 4 weeks, and intermediate leaves had intermediate  $S_{gs}$  values (Table 2 and Fig. 2). There was no difference in G or R among the positions on these dates. By FB + 6 weeks, and for the remainder of the season intermediate and exterior leaves had greater  $S_{gs}$  values than the interior leaves, and G and R remained equal among all three positions. Pseudo  $R^2$  were  $\geq 0.93$  for the regression curves for all dates and positions. Maximum WUE ranged from 3.2 to  $5.7 \mu\text{mol CO}_2 \cdot \text{mmol H}_2\text{O}^{-1}$  during the season, and was equivalent among the three canopy positions on all dates. There was no apparent increasing or decreasing trend in WUE throughout the season (data not presented).

Percent incident PPF measured next to the spurs was greatest at the exterior position on all dates (Table 3). The interior and intermediate positions did not statistically differ, although there was a trend for greater %IPPF at the intermediate position on all dates. %IPPF decreased to a minimum by about FB + 6 weeks, and remained similar for the remainder of the season. Statistical differences in SLW were evident by FB + 2 weeks and for the remainder of the season. Exterior leaves had greater SLW, and interior and intermediate leaves were statistically equivalent, although there was a trend for greater SLW at the intermediate position. SLW increased throughout the season for all of the positions.

Fig. 2. Light response curves of 'Delicious' spur leaves for stomatal conductance ( $g_s$ ) measured at full bloom (FB), FB + 2 weeks, FB + 10 weeks, and FB + 18 weeks. McArthur-Wilson equilibrium equations represent the interior ( $\square$ , - · - · -), intermediate ( $\Delta$ , - - -), and exterior (\*, ———) canopy positions. See Table 2 for equations and coefficients.

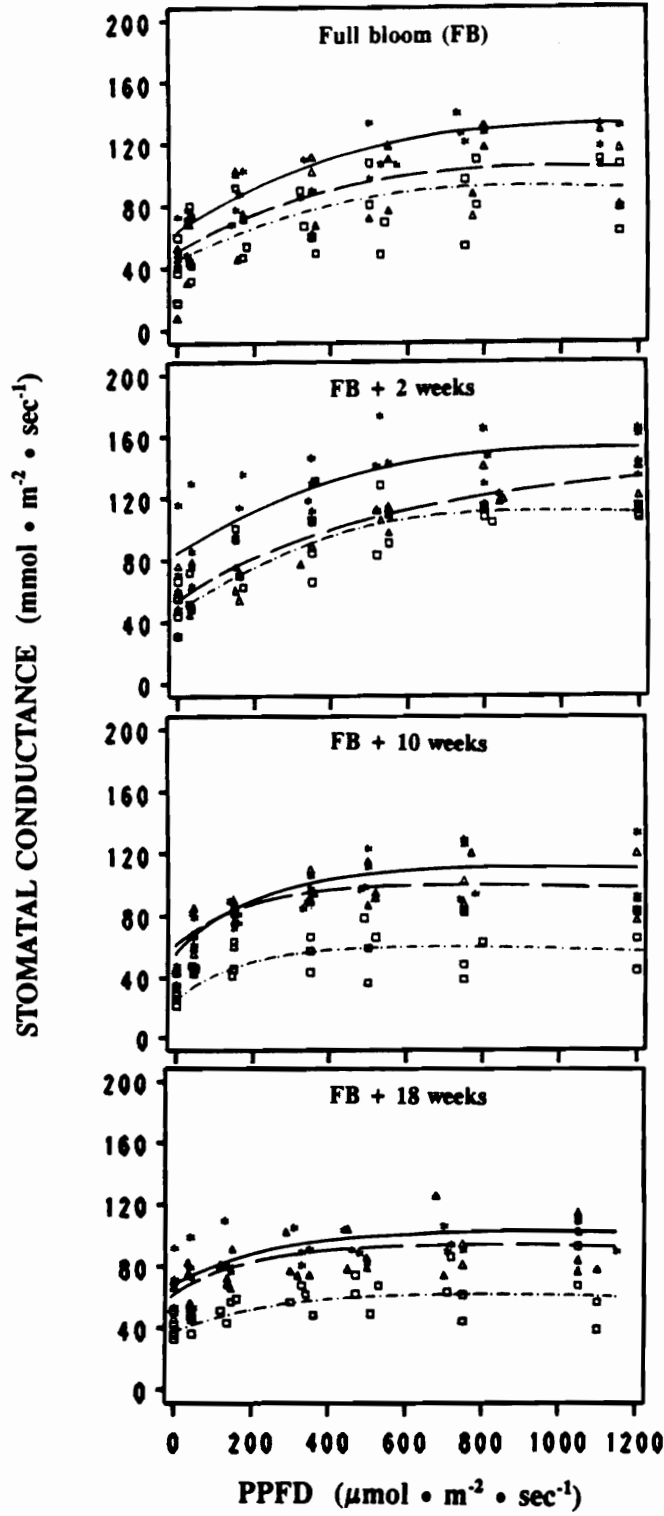


Table 3. Percent incident photosynthetic photon flux density (%IPPF), specific leaf weight (SLW), and dark respiration (Rd) of 'Delicious' leaves from interior, intermediate, and exterior canopy positions.<sup>2</sup>

Canopy Position	IPPF (%)	SLW (mg·cm <sup>-2</sup> )	Rd (μmol·m <sup>-2</sup> ·sec <sup>-1</sup> )
<i>Full Bloom (FB)</i>			
Interior	61 a	5.4 a	1.0 a
Intermediate	69 a	5.1 a	1.1 a
Exterior	89 b	6.2 a	1.8 b
<i>FB + 2 weeks</i>			
Interior	34 a	4.7 a	1.2 a
Intermediate	41 a	4.9 a	1.4 a
Exterior	84 b	6.2 b	1.8 b
<i>FB + 4 weeks</i>			
Interior	16 a	5.6 a	0.8 a
Intermediate	17 a	5.7 a	0.9 a
Exterior	70 b	7.2 b	1.5 b
<i>FB + 6 weeks</i>			
Interior	8 a	5.5 a	0.4 a
Intermediate	15 a	6.1 a	0.6 a
Exterior	66 b	7.8 b	1.3 b
<i>FB + 10 weeks</i>			
Interior	6 a	5.6 a	0.3 a
Intermediate	12 a	6.1 a	0.5 a
Exterior	64 b	9.4 b	1.1 b
<i>FB + 14 weeks</i>			
Interior	8 a	6.1 a	0.2 a
Intermediate	12 b	6.6 a	0.6 a
Exterior	60 a	9.7 b	1.2 b
<i>FB + 18 weeks</i>			
Interior	7 a	6.1 a	0.2 a
Intermediate	13 a	6.7 a	0.5 a
Exterior	65 b	10.4 b	1.1 b
<i>FB + 22 weeks</i>			
Interior	7 a	6.1 a	0.4 a
Intermediate	11 a	6.9 a	0.7 a
Exterior	61 b	10.5 b	1.3 b

<sup>2</sup> Means within columns and dates followed by the same letter do not differ at the 5% level, by Tukey's HSD (n=4).

Dark respiration (Rd) was greatest for the exterior leaves on all dates. After FB + 2 weeks, Rd tended to decrease for all three positions until FB + 18 weeks, and then increased again on FB + 22 weeks.

### Discussion

Reductions in maximum Pn of 50% were reported for leaves of many species grown in low-light environments (Bazzaz and Carlson, 1982; Kappel and Flore, 1983; Nobel, 1976). Barden (1974; 1977) reported that maximum Pn (measured at saturating light levels) of apple leaves grown in an artificially-imposed low-light environment of 20% full sun was 70% of that for leaves from a high-light environment. Under natural shade conditions within an apple canopy, interior leaves had only 70% of the maximum Pn rate of the exterior leaves (Heinicke, 1966). Porpiglia and Barden (1980) measured maximum Pn of spur leaves from different positions within 'Stayman' apple canopies throughout the season. At saturating light levels maximum Pn of interior leaves was about 75% of that for exterior leaves through 8 weeks after FB; similar reductions in maximum Pn of interior leaves were found for 'Stayman' and 'Delicious' in our study. Measurements made by Porpiglia and Barden (1980) at 14 and 20 weeks after FB demonstrated a marked decline in Pn of the interior leaves, while Pn of the exterior leaves declined only slightly, resulting in interior leaves with 55 to 60% of the Pn rate of exterior leaves. Our data had the

same trend, and by FB + 10 weeks until the end of the season the maximum Pn of the interior leaves was 50 to 60% of that for the exterior leaves.

In addition to maximum Pn, light response curves for Pn differed for low- and high-light leaves of apple (Barden, 1977), *Ficus benjamina* (Fails et al. 1982b), and peach (Kappel and Flore, 1983). Within mature citrus (Syvertson, 1984) and mango (Schaffer and Gaye, 1989) canopies there were differences in Pn light response curves between interior and exterior leaves. Our results agree with these previous studies in the general shape of the Pn light response curves for the leaves from the different canopy positions. Although maximum Pn ( $S_{Pn}$ ) and rates of approach to equilibrium Pn ( $G$ ) changed over the season, the basic curve shape and the relationship among the positions was similar throughout the season. In general, 'Stayman' and 'Delicious' had similar responses throughout the season; however, the interior and intermediate 'Stayman' leaves had coincident light response curves after FB + 2 weeks, while light response curves differed for these positions within the 'Delicious' canopy. This may have been due to increased shading within the 'Stayman' trees because they were larger, although light levels were not measured to confirm this. The similarity of interior and intermediate leaves also indicates that the transitional zone between interior and exterior leaves (intermediate position) is relatively narrow and close to the periphery of the canopy.

Use of indicator variables with MacArthur-Wilson equilibrium equations was advantageous because it allowed statistical comparison of the entire light response

curve, and we were therefore able to determine whether two light response curves differed from each other. Previous researchers with tree fruits often fitted the data by eye with no statistical comparison, or separations were made at discrete points along the response curve (Barden, 1977; Syvertson, 1984). Such methods yield no information about the rate of approach to equilibrium ( $G$ ), as is possible with the McArthur-Wilson equilibrium equations. For example, if the maximum  $P_n$  rates ( $S_{P_n}$ ) were equivalent for two sets of leaves,  $G$  could be used as an indicator of quantum efficiency. McArthur-Wilson equilibrium equations have more biological relevance than quadratic equations because they lack the decrease in response at greater light levels found with quadratic equations. MacArthur-Wilson equations have the disadvantage of not fitting the  $R_d$  portion of the curve due to the limitations of the exponential equation, so light compensations points cannot be directly determined with these equations.

Enhanced quantum efficiency at sub-saturating light levels was reported for leaves from low-light environments with citrus (Syvertson, 1984), *Ficus benjamina* (Fails et al., 1982b), peach (Kappel and Flore, 1983), and *Fragaria vesca* (Chabot and Chabot, 1977) although data were statistically analyzed only for citrus. In contrast, Fig. 1 demonstrates that on any date in our study, the exterior leaves had an equal or greater quantum efficiency (nonsignificant trend) than the intermediate or interior leaves at all PPFD levels. Therefore, our data suggest that the exterior leaves would fix more carbon at any PPFD level compared to interior or intermediate leaves. In

agreement with our results, Schaffer and Gaye (1989) reported that high-light mango leaves had greater quantum efficiency at sub-saturating light levels than low-light leaves, and no statistical difference in quantum efficiency was reported for other plant species from low- and high-light environments (Bjorkman and Holmgren, 1963; Mahall and Schlesinger, 1982). Some of the reported differences in quantum efficiency are probably due to the lack of statistical comparison, but it may also differ with plant species considered, as Bazzaz and Carlson (1982) reported considerable variation in the relationship between low- and high-light leaves among plant species.

Anatomical differences in the leaves due to the light environment probably contributed in part to the reductions in Pn potential of the interior and intermediate leaves, as evidenced by the suppression of SLW at these positions. Previous studies with many plant species demonstrated that leaves grown in a low-light environment were thinner and larger, with lower SLW and a thinner poorly-developed palisade layer, while leaves from a high-light environment were thicker and smaller, with greater SLW and a thicker well-developed palisade layer (Chabot and Chabot, 1977; Fails et al. 1982a; Jackson and Palmer, 1977; Mahall and Schlesinger, 1982; Wooge and Barden, 1987). Seasonal trends and values of SLW were similar to those previously reported for apple (Marini and Barden, 1981; Porpiglia and Barden, 1980). Marini and Barden (1981) reported that SLW was correlated with Pn potential throughout the season ( $R^2 \geq .49$ ), with the poorest relationships early and late in the

season. Rd rates and trends throughout the season were similar to those previously reported for apple (Marini and Barden, 1981; Porpiglia and Barden, 1980).

Alteration of the Pn response could be due in part to a stomatal limitation to CO<sub>2</sub> diffusion ( $g_s$ ), because the interior position had  $g_s$  rates only 50-70% of that for the exterior position. Reduced leaf conductance to water was reported for *Ficus benjamina* (Fails et al., 1982b) and chaparral shrub (Mahall et al., 1981) leaves grown in low-light environments, and Schaffer and Gaye (1989) reported reduced  $g_s$  for interior canopy leaves of mango. The reduced  $g_s$  of the interior leaves may be due to a suppression of stomatal density of these leaves, as previously reported in *Ficus benjamina* (Fails et al., 1982a), and *Sinapis alba* (Wild and Wolf, 1980). Mahall and Schlesinger (1982) reported that WUE was greater for chaparral shrub leaves from a high-light environment, and this was also reported for citrus leaves (Syvertson, 1984). However, in agreement with our results, no effect of light environment on WUE was reported for mango leaves (Schaffer and Gaye, 1989).

Unless leaves at interior positions were predisposed to an inferior gas exchange capacity due to the previous season's light environment, the reduction in available light from 89 to 61% IPPFD at FB, although relatively small, had a significant influence on gas exchange capacity of the leaves. We are unaware of other studies measuring Pn potential of spur leaves this early in the season for comparative purposes. The influence of the previous season's light environment on early-season Pn potential deserves further study, and the results may lead to changes

in canopy management practices. The apple canopy late in the season has been described as possessing two distinct zones of Pn potential: a thin exterior canopy with greater maximum Pn potential and an interior canopy with a lesser maximum Pn potential (Heinicke, 1966). Our results indicate that the exterior canopy leaves also possess distinct Pn and  $g_s$  light response curves throughout the season, and a tendency for greater quantum efficiency at sub-saturating PPFD levels than the interior canopy. For precise whole-canopy modelling and cultural techniques designed to manage the physiology of the canopy as related to light, these gas exchange characteristics of the leaves should be considered.

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### Chapter III

#### Instantaneous Light Measurements Predict Relative Cumulative Light Levels Within an Apple Canopy

*Abstract.* Percent instantaneous incident photosynthetic photon flux density (%INPPFD) was measured within an apple canopy for different sky conditions and used to predict the percent cumulative incident photosynthetic photon density for the last 10 weeks of the growing season (%CPPD<sub>LS</sub>) and the total growing season (%CPPD<sub>TS</sub>). Instantaneous measurements from overcast conditions were superior to measurements from clear or hazy conditions for the prediction of %CPPD<sub>LS</sub> in 1989 and 1990. A 1-to-1 relationship between %INPPFD and %CPPD<sub>LS</sub> was found for overcast conditions in both years, even though there was an 11% difference in total cumulative photosynthetic photon density between the years. The models had good predictive accuracy, with  $R^2_{\text{Pred}}$  greater than 0.83 in both years ( $n = 30$ ). %INPPFD from overcast conditions also yielded accurate predictive models for %CPPD<sub>TS</sub> ( $R^2_{\text{Pred}} > 0.84$ ,  $n = 30$ ), which differed from the models for %CPPD<sub>LS</sub>. Predictive models (for both %CPPD<sub>LS</sub> and %CPPD<sub>TS</sub>) from %INPPFD made before the canopy was fully-developed differed from the models developed after canopy development was complete. The models still had good predictive accuracy, with  $R^2_{\text{Pred}} > 0.76$  ( $n = 30$ ). Predictive models developed for cloudless conditions had inferior predictive accuracy ( $R^2_{\text{Pred}} = 0.49$  to  $0.80$ ,  $n = 30$ ) compared to models for overcast conditions.

$R^2_{\text{Pred}}$  were greater for hazy compared to clear conditions. Time of day (1000 to 1400 hr) had no consistent effect on the development of predictive models for any weather condition. The most reliable models resulted from the average of several measurements within a day, particularly for cloudless conditions.

## Introduction

Many instruments and measurement techniques have been used to characterize the light environment of plant communities and individual tree canopies (Anderson, 1964a; Jackson, 1980). The introduction of the quantum sensor allowed for the relatively quick and simple selective measurement of the photosynthetically active waveband 400-700 nm, expressed as a photosynthetic photon flux density (PPFD). Instantaneous measurements with quantum sensors (and other instruments) have been used extensively for light environment studies within tree canopies, and have been related to spur, leaf, and fruit quality characteristics within the canopy (Barritt et al., 1987; Marini and Barden, 1982; Marini and Marini, 1983; Morgan et al., 1984; Patten and Proebsting, 1986). Instantaneous light measurements, often based on only a few measurements during the season, have been used to represent total seasonal (cumulative) light levels. The validity of instantaneous measurements as estimates of total cumulative light levels has been questioned due to the complicated nature of canopy/light interactions, such as weather variations, proportions of direct and diffuse light, sunflecks, spectral changes, and the timing of measurements (Anderson, 1964a, Monselise, 1951).

For the measurement of PPFD, Grappadelli and Coston (1988) described the construction of an inexpensive silicon photocell sensor, which had a similar measurement response to commercially-produced quantum sensors. Combined with a datalogger, these sensors provide an affordable method of measuring the total

cumulative photosynthetic photon density (PPD) impinging upon multiple canopy positions throughout the season, and an opportunity to relate these total cumulative PPD values to predicted cumulative PPD values derived from instantaneous measurements.

The objectives of this study were to test the validity of instantaneous measurements as predictors of total cumulative PPD, and to determine what sky conditions and measurement techniques yield the most reliable estimates.

### **Materials and Methods**

*Sensor construction and calibration.* Silicon photocell sensors were constructed according to the design of Grappadelli and Coston (1988). The sensor body consisted of a clear plexiglass base with a 13×32×4 mm depression routed-out for the placement of a 1×2 cm silicon photocell (Texas Optoelectronics Inc., Garland, TX) and a glass filter which excluded wavelengths below 400 and above 700 nm (B638, Schott Optical Glass Inc., Duryea, PA). Plasti-tak (Brooks Manufacturing Co., Cincinnati, OH) secured the sensor and filter firmly in the depression. A lucite-L cast acrylic top (E. I. Du Pont De Nemours & Co., Inc. Wilmington, DE) was then glued onto the base covering the filter and sensor, and sealed with silicon rubber. The cast acrylic top (diffusive material) provided some degree of "cosine" correction. The entire sensor was covered with plastic electrician's tape except for a 1×2 cm window directly above the filter and silicon photocell allowing light to enter. Eight

meters of 24-gauge coated wire was soldered to the sensor leads, and a 100-ohm, 20-turn trimmer potentiometer was spliced into the wire for standardization of sensor output. The sensors were connected to a 21X data logger (Campbell Scientific, Inc., Logan, UT) through a 32-channel multiplexer (Model AM32, Campbell Scientific, Inc.). The sensors were standardized against a Lambda quantum sensor (Model LI190SB, LI-COR, Lincoln, NE) on a cloudless day by adjusting the potentiometer until the millivolt output was equal to the output of the quantum sensor. Sensors were then compared to the quantum sensor over a range of light levels to ensure a linear response.

*Orchard.* The study was conducted in 1989 and 1990 at the Virginia Polytechnic Institute and State Univ. Horticulture Farm in Blacksburg, VA. Two 14-year-old 'Red Prince Delicious'/MM.111 trees were used, with an average height and width of 5.4 and 4.8 m, respectively; average trunk circumference was 60 cm. The east-west rows were spaced at 5.5 m in-row and 6.1 m between-rows.

*Sensor placement.* Twenty-three silicon photocell sensors were placed within one of the 'Delicious' trees in 1989, and 15 sensors were placed in each of the two trees (30 total sensors) in 1990. The silicon photocell sensors were placed in close proximity to fruit within the canopy for use in another study (see Chapter IV). Sensor (canopy) positions were chosen to provide a wide range of light levels. The sensors were taped to 1.9×3.8 cm wooden furring strips with electricians tape, and the furring strips were nailed at varying heights onto 4.6 m-high, 5×10 cm wooden boards

(3 to 5 sensors per board). There were five boards placed within the canopy of each tree, one immediately adjacent to the trunk, and the remaining four in either the NE, NW, SE, or SW quadrants of the tree, respectively, about 50 to 100 cm within the periphery of the canopy. The sensors were levelled and periodically adjusted to ensure they remained horizontal. The sensors were oriented to the southern-side of the boards so there was no direct shading of sensors from the boards themselves. For ambient (incident) PPF<sub>D</sub> measurements, and comparison of the two sensor types, one silicon photocell sensor and one Lambda quantum sensor were placed side-by-side on a 4.6 m pole in the row where two trees had been removed.

*Cumulative light measurements.* The datalogger was programmed to record the PPF<sub>D</sub> at each sensor position at 10-sec intervals from 0600 to 2100 hr EST. These data were stored as 5-min PPD totals in 1989, and as 15-min PPD totals in 1990 and expressed in quantum units,  $\text{mmol} \cdot \text{m}^{-2}$ . The data were transferred to a computer and summed for cumulative PPD totals with SAS (SAS, 1985). Percent cumulative incident PPD was calculated by dividing the cumulative total PPD for each position by the cumulative total incident PPD. PPD was recorded from 22 July to 4 October in 1989 and termed percent cumulative incident late-season PPD ( $\%CPPD_{LS}$ ). PPD was measured from March 23 to October 4 in 1990 and the percent cumulative incident total-season PPD ( $\%CPPD_{TS}$ ) was calculated. A second data set with  $\%CPPD_{LS}$  was also calculated for 1990 over the same dates used in the previous year.

*Instantaneous light measurements.* Instantaneous measurements were made on overcast and cloudless days. Cloudless days were differentiated into clear and hazy days in 1990 based on the average amount of diffuse PPFD available for that day; clear days had an average of less than  $300 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  diffuse PPFD, and hazy days had between  $500\text{-}700 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  of diffuse PPFD. Diffuse PPFD was measured by shading the incident sensor with a  $10 \text{ cm}^2$  disc to block the direct rays of light. Instantaneous PPFD measurements were made hourly between 1000 and 1400 hr on three overcast and three hazy days in 1989 by keying through all 23 channels of the datalogger and recording the PPFD level at that instant. Each series of instantaneous measurements was completed in less than 60 sec. Incident PPFD was also recorded at each hourly measurement for the calculation of percent instantaneous incident PPFD values (%INPPFD). In 1990, hourly %INPPFD readings were made between 1100 and 1400 hr with the silicon photocell sensors at all 30 positions within the two trees on two clear, two hazy, and six overcast days. Each series of measurements was completed in less than 90 sec. %INPPFD were also measured at 20 of the 30 total sensor positions (selected to provide a wide range of light levels) on each measurement day in 1990 with a Lambda quantum sensor by holding the sensor in a horizontal position directly above the silicon photocell sensor. These measurements were completed in less than 4 min.

*Light distribution patterns within the canopy.* Fifteen-minute PPD totals throughout the day are presented for selected sensor positions for clear (13 August)

and overcast (28 September) conditions in 1990 for comparisons of light distribution or sunfleck patterns within the canopy. The peripheral (40 cm from top of tree), intermediate (250 cm from top), and interior (480 cm from top) canopy positions were located from the top to the bottom of the board adjacent to the trunk of a single tree (within 40 cm of trunk). Incident PPD totals are presented for reference levels.

*Statistical analysis (Model development).* Hourly %INPPFD were averaged for each measurement day and regressed against %CPPD<sub>LS</sub> in 1989 and 1990, and against %CPPD<sub>TS</sub> in 1990. Regression models for %INPPFD and %CPPD<sub>LS</sub> were also developed for the individual hourly measurements within each day to determine what time of the day (if any) yielded the best model. Pooled models were developed based on all data (multiple measurement days) for each particular weather condition within each year. Both fitting criteria ( $R^2_{\text{Fit}}$ ), and prediction criteria ( $R^2_{\text{Pred}}$ ) are presented for each predictive model. The  $R^2_{\text{Pred}}$  is calculated from the prediction error sum of squares, which is considered a form of data-splitting (Montgomery and Peck, 1982). This statistic provides an indication of the predictive accuracy of a given model. Models were compared among days within each year and between years with indicator variables in multiple regression (Montgomery and Peck, 1982). Models were judged to be statistically different if either the slope or the intercept differed at the 5% level.

## Results

*Silicon photocell measurement response.* Biggs et al. (1971) demonstrated that significant error could occur when a flat diffusive plexiglass surface was used to measure light at angles greater than 30 degrees from the vertical (cosine response), and Grappadelli and Coston (1988) discussed this as a potential problem with their design of a silicon photocell sensor. For our field conditions, however, the error induced by solar angle had little effect on the relationship between the silicon photocell sensor and the quantum sensor. There was some evidence of a relatively greater discrepancy between the two sensors at extreme solar angles (early morning and late evening), but PPFD accumulations at these times were almost negligible and therefore not an appreciable source of error for total cumulative PPD measurements (data not presented). There was a 1-to-1 relationship (intercept=0 and slope=1) between the silicon photocell sensor and the quantum sensor for all sky conditions (overcast, hazy, or clear), with  $R^2$ 's above 0.98 in all cases (data not presented).

*Cumulative late-season PPD, overcast conditions.* Predictive models for %CPPD<sub>LS</sub> developed from %INPPFD during overcast conditions in 1989 fit the data better ( $R^2_{\text{Fit}}$ ) and had superior predictive accuracy ( $R^2_{\text{Pred}}$ ) than models developed for hazy conditions (Table 1). The models for the overcast conditions were equivalent among all three days tested, with similar degrees of predictive accuracy.

Table 1. Predictive models for the relationship between percent instantaneous incident PPF<sub>D</sub> measurements (%INPPFD) and percent cumulative incident PPD measurements for the latter part of the season (%CPPD<sub>LS</sub>), 22 July - 4 October, 1989. Model: %CPPD<sub>LS</sub> = a + b (%INPPFD).

Sky condition	Date	Model coefficients			R <sup>2</sup>	R <sup>2</sup>
		Intercept	Slope		Fitting	Prediction
Hazy	August 6	8	.78	a <sup>z</sup>	.84	.80
	August 7	10	.69	a	.84	.80
	August 8	11	.61	a	.82	.79
	<b>Pooled</b>	<b>10</b>	<b>.68</b>	<b>a</b>	<b>.83</b>	<b>.81</b>
Overcast	August 25	3	.97	b	.96	.95
	August 26	4	.95	b	.94	.92
	August 27	2	.98	b	.97	.96
	<b>Pooled</b>	<b>2</b>	<b>.97</b>	<b>b</b>	<b>.96</b>	<b>.96</b>

<sup>z</sup> Models were compared with indicator variables and were determined to be different if the slopes differed. Models followed by the same letter do not differ at P < 0.05 (n = 30). All slopes differed from zero at P < 0.01.

There was nearly a 1-to-1 relationship (intercept = 2 to 4, and slope = 0.95 to 0.98) between %INPPFD and %CPPD<sub>LS</sub> for each individual day and for the pooled model for overcast conditions. Predictive models for %CPPD<sub>LS</sub> developed for overcast conditions after June 15 in 1990 were equivalent to the models developed in 1989; again there was nearly a 1-to-1 relationship (intercept = 0 to 2, and slope = 1.0 to 1.04) between %INPPFD and %CPPD<sub>LS</sub> (Table 2). The predictive models were equivalent for the overcast days from 15 June through 22 August, 1990. The actual %INPPFD data for a typical overcast day in 1990 closely fit the pooled predictive model over the entire range of measured PPFD levels (Fig. 1a).

Predictive models developed from %INPPFD for overcast conditions early in the season (before June 15) differed from the models that were developed on the days later in the season (Table 2). The model for March 30 had an intercept of -116% and a slope of 1.83, but the model still had a relatively good predictive value, with an  $R^2_{\text{Pred}}$  of 76%. The highly negative intercept and slope > 1 indicate that the model accounted for the higher light levels within the canopy when the trees were at the green-tip developmental stage. Since the canopy was still not fully developed by April 30, the predictive model for %CPPD<sub>LS</sub> still had a negative intercept and a slope > 1, but the model was more similar to the models developed after the canopy was fully developed. Predictive models and data points for measurements from 30 March, 30 April, and 8 August, 1990 for overcast conditions are presented in Fig. 2.

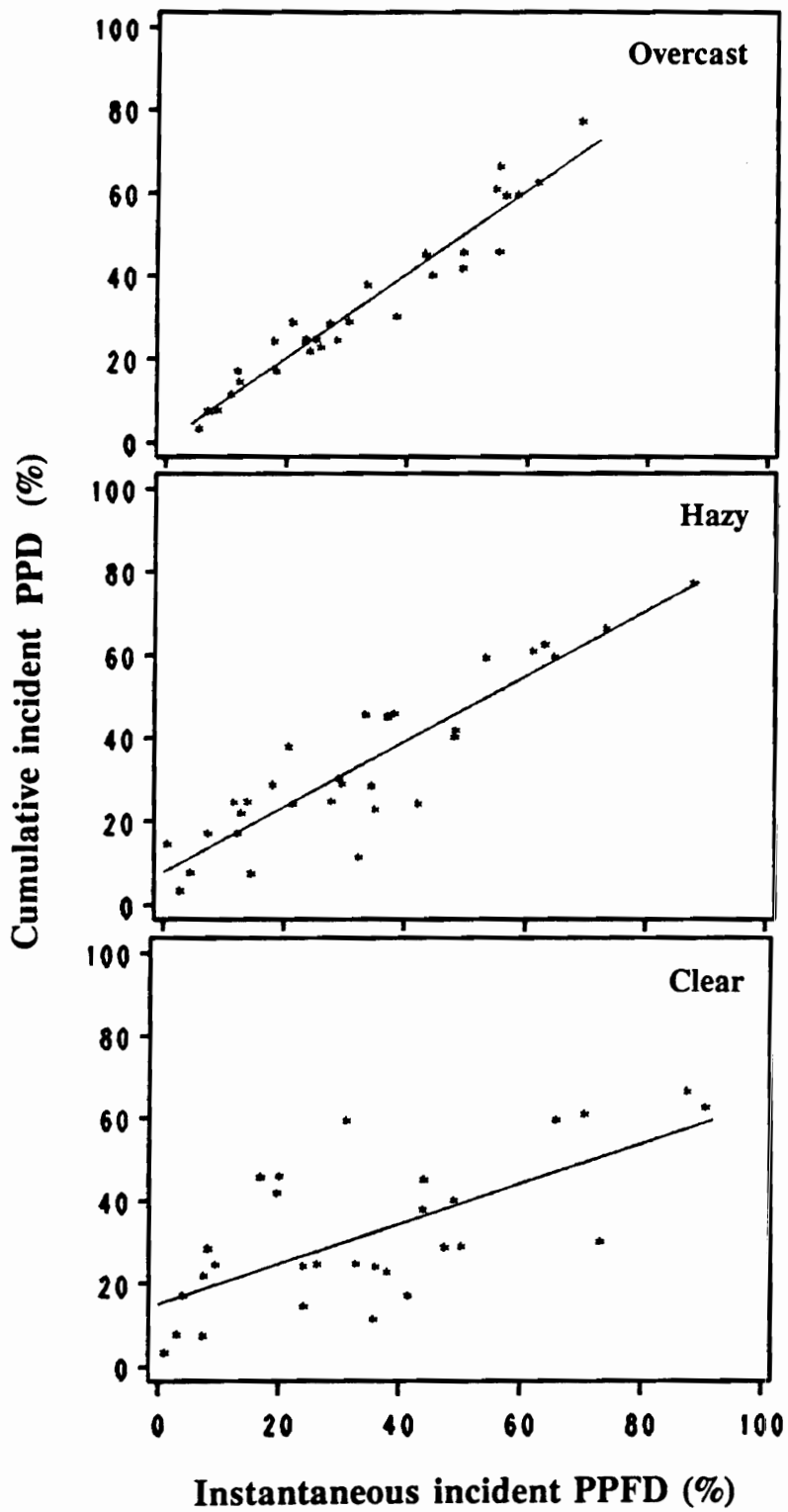
Table 2. Predictive models for the relationship between percent instantaneous incident PPF<sub>D</sub> measurements (%INPPFD) and percent cumulative incident PPD measurements for the latter part of the season (%CPPD<sub>LS</sub>), 22 July - 4 October, 1990. Model: %CPPD<sub>LS</sub> = a + b (%INPPFD).

Sky conditions	Date	Model coefficients			R <sup>2</sup>	R <sup>2</sup>
		Intercept	Slope		Fitting	Prediction
Clear	May 7	14	.53	a <sup>z</sup>	.57	.51
	August 7	14	.52	a	.54	.49
	<b>Pooled</b>	<b>14</b>	<b>.52</b>	<b>a</b>	<b>.56</b>	<b>.53</b>
Hazy	June 12	10	.79	a	.75	.74
	July 10	8	.78	a	.81	.80
	<b>Pooled</b>	<b>9</b>	<b>.78</b>	<b>a</b>	<b>.79</b>	<b>.76</b>
Overcast	March 30	-116	1.83	b	.79	.76
	April 30	-19	1.17	c	.83	.80
	June 15	2	1.04	d	.85	.83
	August 8	0	1.03	d	.90	.89
	August 22	1	1.00	d	.90	.88
	<b>Pooled<sup>y</sup></b>	<b>1</b>	<b>1.01</b>	<b>d</b>	<b>.90</b>	<b>.89</b>

<sup>z</sup> Models were compared with indicator variables and were determined to be different if the slopes differed. Models followed by the same letter do not differ at P < 0.05 (n = 30). All slopes differed from zero at P < 0.01.

<sup>y</sup> Pooled model based on June 15, August 8, and August 22 data only.

Fig. 1. Relationship between percent cumulative incident PPD and percent instantaneous incident PPFd for different sky conditions (n = 30). a) Plotted data for 8 August (overcast) and pooled regression model for overcast conditions, 1990:  $\%CPPD_{LS} = 1 + 1.01 (\%INPPFD)$ ,  $R^2 = 0.90$ . b) Plotted data for 10 July, (hazy) and pooled model for hazy conditions, 1990:  $\%CPPD_{LS} = 9 + 0.78 (\%INPPFD)$ ,  $R^2 = 0.76$ . c) Plotted data for 7 August (Clear) and pooled regression model for clear conditions, 1990:  $\%CPPD_{LS} = 14 + 0.52 (\%INPPFD)$ ,  $R^2 = 0.53$ .



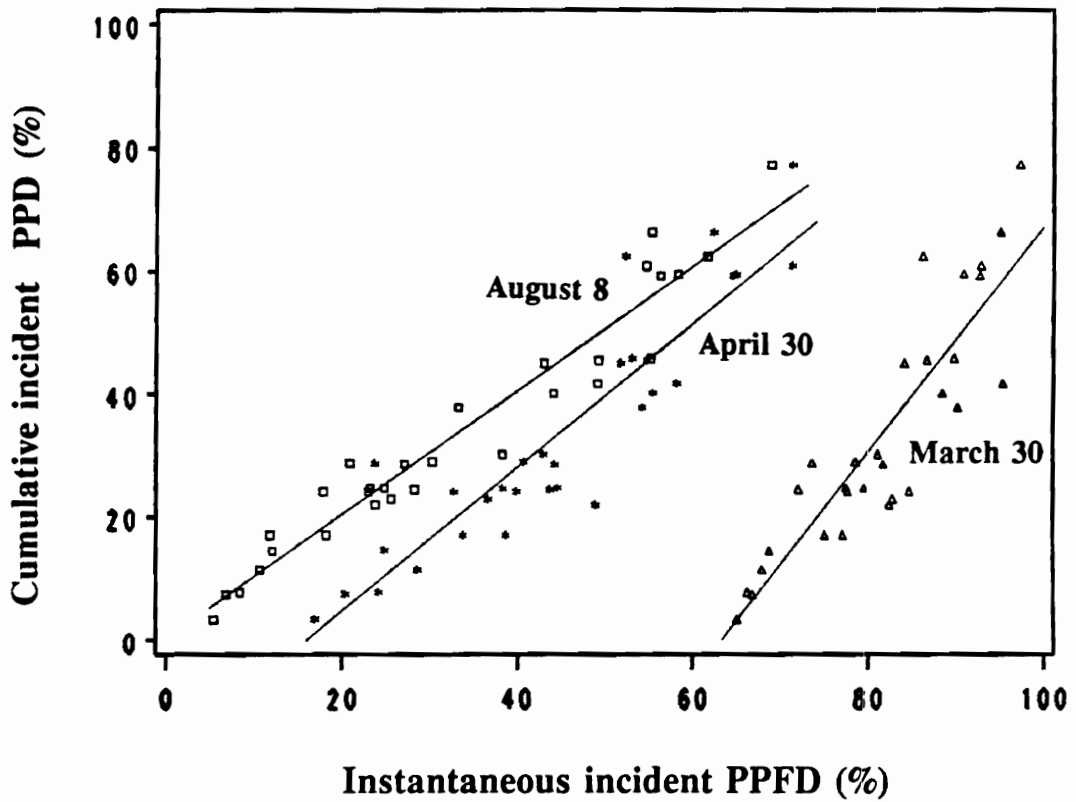


Fig. 2. Relationship between percent cumulative incident  $PPD_{LS}$  and percent instantaneous incident PPF D for three overcast days in 1990; 30 March ( $\Delta$ ), 30 April (\*), and 8 August ( $\square$ ). Models are presented in Table 2.

***Cumulative late-season PPD, cloudless conditions.*** The predictive models developed for hazy conditions differed from the models developed for overcast conditions in both 1989 and 1990 (Tables 1 and 2). The predictive models were equivalent among the hazy days within both years, with similar degrees of accuracy. The predictive models were also equivalent between the two years (pooled models). Models for the hazy conditions had a poorer fit to the data and predictive capability compared to the models for the overcast conditions, but  $R^2_{\text{Pred}}$  was still nearly 80% in most cases. The variation around the regression line was clearly greater for hazy conditions (Fig. 1b) as compared to the overcast conditions (Fig. 1a). Predictive models developed for clear conditions were statistically equivalent to the models developed for hazy conditions, but the models developed for clear conditions had poorer fitting and prediction criteria compared to the other models, with  $R^2_{\text{Pred}}$  of about 50%. The large variation around the predicted line for clear days is evident in Fig. 1c.

***Cumulative total-season PPD.*** The previous results concerned using %INPPFD measurements to predict %CPPD<sub>LS</sub>, or the total cumulative light over the last 10 weeks of the season. Such estimates of total light over this time period could be useful for correlating light with fruit quality characteristics, such as red color development (Barritt et al., 1987; Lakso, 1980; Seeley et al., 1980). However, it may also be of interest to use %INPPFD to predict %CPPD<sub>TS</sub>, or cumulative light over the entire growing season. The predictive models for %CPPD<sub>TS</sub> differed from the

models for %CPPD<sub>LS</sub> (Table 3), but the models had the same separation trend over the season. In general, the predictive models for %CPPD<sub>TS</sub> had similar  $R^2_{\text{Fit}}$  and  $R^2_{\text{Pred}}$  to those for the %CPPD<sub>LS</sub> predictive models. After the canopy was fully developed (after June 15) the intercept was  $\approx 13$  and the slope 0.80. Models developed to estimate total-season cumulative PPD values differed from models for late-season cumulative PPD values because %INPPFD were measured when the canopy was fully developed and light levels within the canopy were low, but these interior positions had accumulated significant PPD before the canopy was fully developed. Therefore, the intercept should not have approached 0. %INPPFD made at green-tip developmental stage (March 30) and a month later (April 30) gave reliable estimates of total season light levels and had better predictive value for %CPPD<sub>TS</sub> than they had for %CPPD<sub>LS</sub>, probably because they more accurately accounted for the early-season light.

*Time of day.* For hazy conditions, the models developed between %INPPFD and %CPPD (LS or TS) for each measurement time within a day varied in predictive value, with no time between 1000 and 1400 hr clearly superior for the prediction of %CPPD<sub>LS</sub> (Table 4). Within a hazy day, there were both strong and weak relationships, with  $R^2_{\text{Pred}}$  ranging from 17 to 86%. There was an improvement in the  $R^2_{\text{Pred}}$  for hazy conditions when the measurement times were averaged (pooled model). For overcast conditions there was typically little variation in  $R^2_{\text{Pred}}$

Table 3. Predictive models for the relationship between percent instantaneous incident PPFd measurements (%INPPFD) and percent cumulative incident PPD measurements for the entire season (%CPPD<sub>TS</sub>), 23 March - 2 October, 1990. Model: %CPPD<sub>TS</sub> = a + b (%INPPFD).

Sky conditions	Date	Model coefficients			R <sup>2</sup>	R <sup>2</sup>
		Intercept	Slope		Fitting	Prediction
Clear	May 7	22	.45	a <sup>z</sup>	.63	.58
	August 7	24	.41	a	.50	.44
	<b>Pooled</b>	<b>23</b>	<b>.43</b>	<b>a</b>	<b>.56</b>	<b>.54</b>
Hazy	June 12	19	.65	a	.79	.74
	July 10	18	.65	a	.84	.81
	<b>Pooled</b>	<b>19</b>	<b>.65</b>	<b>a</b>	<b>.76</b>	<b>.75</b>
Overcast	March 30	-87	1.55	b	.86	.83
	April 30	-5	.99	c	.89	.88
	June 15	13	.88	d	.91	.90
	August 8	13	.83	d	.86	.84
	August 22	13	.80	d	.86	.84
	<b>Pooled<sup>y</sup></b>	<b>13</b>	<b>.81</b>	<b>d</b>	<b>.86</b>	<b>.86</b>

<sup>z</sup> Models were compared with indicator variables and were determined to be different if the slopes differed. Models followed by the same letter do not differ at P < 0.05 (n = 30). All slopes differed from zero at P < 0.01.

<sup>y</sup> Pooled model for June 15, August 8, and August 22 data only.

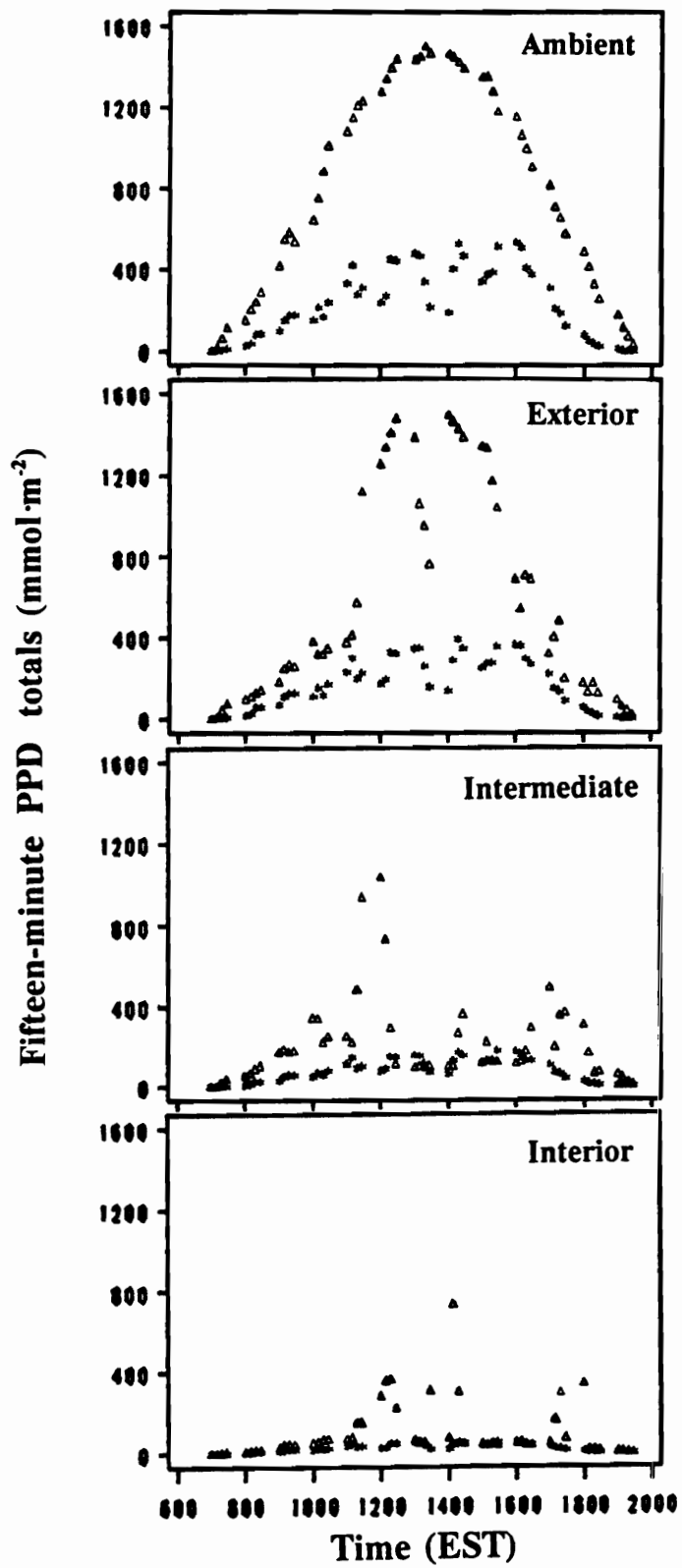
Table 4. Typical variation in the coefficients of determination for regression models between percent instantaneous incident PPFD (%INPPFD) and percent cumulative incident late-season PPD (%CPPD<sub>LS</sub>) for different measurement times within a hazy and an overcast day in 1989.

Sky condition	Date	Eastern standard time	R <sup>2</sup> <sub>Fit</sub>
Hazy	August 8	1000	.76
	August 8	1100	.71
	August 8	1200	.17
	August 8	1300	.86
	August 8	1400	.72
	<b>Pooled</b>	-	<b>.89</b>
Overcast	August 25	1000	.96
	August 25	1100	.96
	August 25	1200	.96
	August 25	1300	.96
	August 25	1400	.96
	<b>Pooled</b>	-	<b>.97</b>

throughout the day; all times between 1000 and 1400 hr yielded equivalent models with similar degrees of accuracy (Table 4). Averaging of multiple measurement times during an individual day was therefore not as important on overcast days.

*Light distribution patterns within the canopy.* Sunflecks were responsible for the variation in the predictive accuracy of the models developed for the multiple measurement times within an individual hazy (or clear) day. Fig. 3 demonstrates the pattern of 15-min PPD accumulations over the course of a clear and an overcast day for selected canopy positions within a single 'Delicious' tree. Ambient PPD totals differed between the overcast and clear days, with a greater variation in the totals on the overcast day. Greater variation due to haze and high altitude cirrus clouds would usually be present for cloudless conditions in Blacksburg, but this uniformly clear day was presented to provide a smooth baseline to illustrate sunflecks. At a peripheral canopy position, PPD totals on the clear day varied significantly due to shading within the canopy, as previously demonstrated (Christopher, 1934; Kromenko, 1972; Proctor et al., 1975); PPD totals for overcast conditions at the peripheral canopy position were lower than ambient, but the variation was similar to ambient because of the influence of diffuse light. At the intermediate canopy position there was a great deal of variation associated with the PPD totals on the clear day, while the PPD totals on the overcast day were low, but relatively stable. At the interior canopy position there was little PPD present on either the clear or

Fig. 3. Fifteen-minute PPD totals for selected sensor positions on a clear day ( $\Delta$ ), 9 August, and an overcast day (\*), 15 August, 1990. a) Incident position; b) Exterior position; c) Intermediate position; d) Interior position.



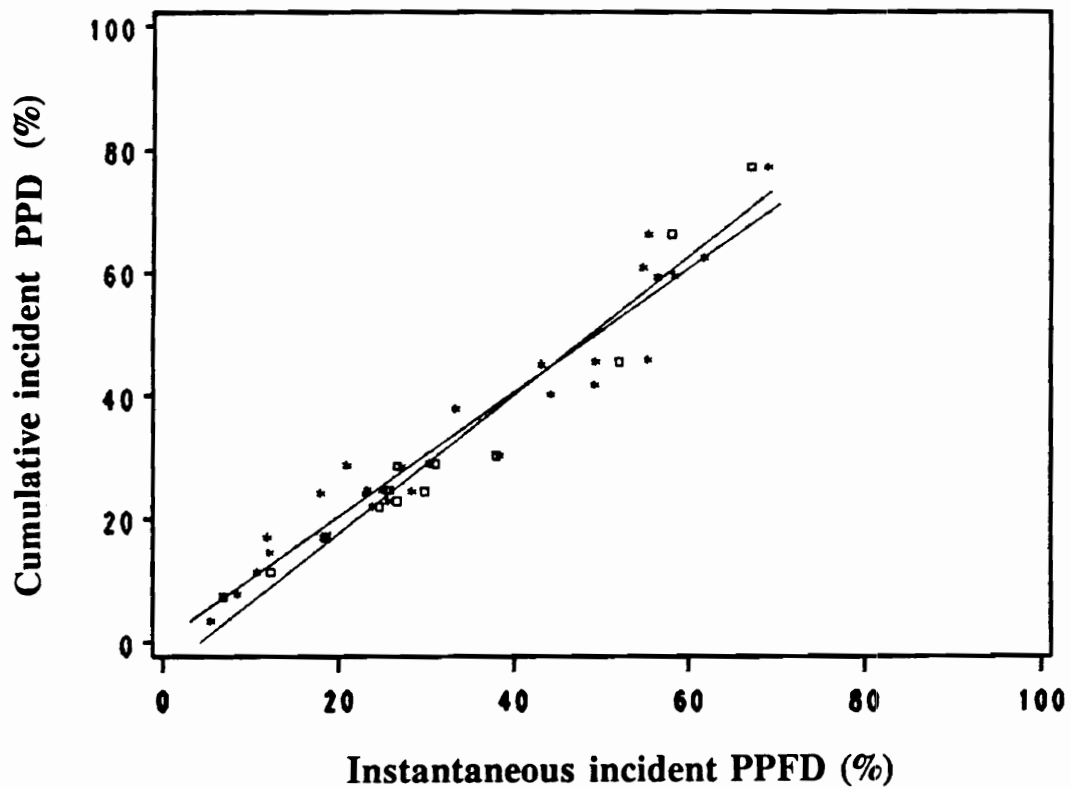


Fig. 4. Relationship between percent cumulative incident PPD and percent instantaneous incident PPFD when measurements were made with silicon photocell sensors (\*) and a quantum sensor (□) on Aug. 8, 1990. Models do not differ at  $P < 0.05$ .

overcast days, except for an occasional sunfleck on the clear day. These plots demonstrate how sunflecks influence instantaneous measurements for clear conditions, and why averaging the measurements within a day is advantageous. For overcast conditions there were no sunflecks; therefore, averaging the measurement times within a day had little effect.

*Silicon photocell vs quantum sensor.* All predictive models presented in this study are based on silicon photocell sensors. Predictive models were also developed with a commercially-produced, hand-held Lambda quantum sensor. In all situations the quantum sensor yielded equivalent models to the models developed with the silicon photocell sensors (Fig. 4), and as with the silicon photocell sensor, overcast conditions yielded the best predictive models compared to hazy or clear conditions. Prediction criteria for these models were usually comparable to those for the silicon photocell sensors. However, because it took more time to complete a series of instantaneous measurements with the quantum sensor, the predictive models were sometimes weaker (lower  $R^2_{\text{Pred}}$ ) when the light conditions changed rapidly during measurements.

## Discussion

The interaction of diffuse and direct light (sunflecks) within plant canopies is a major consideration or concern associated with instantaneous light measurements in plant communities (Anderson, 1964b; Evans et al., 1956; Monselise, 1951). Direct

light is that part of the total solar radiation that travels in a straight line from the sun to the receiving object. Diffuse light is that portion of the solar radiation reflected off clouds, and impurities in the atmosphere and may impinge upon the receiving object from any direction. Direct light is greatest for cloudless conditions, often accounting for 90% of the total radiant energy (Heinicke, 1967). The relative percentage of diffuse light increases with increasing haze or clouds, and may constitute nearly 100% of the total radiant energy for overcast conditions.

In the eastern United States overcast and hazy conditions are prevalent during the growing season, and result in appreciable diffuse light levels throughout the season. Thus, diffuse light should have been a major contributor to the total cumulative light for our study. Anderson (1964c) determined that diffuse light was the major contributor to total cumulative light within a temperate forest in southern England, where overcast and hazy conditions also predominate during the growing season. Therefore, it is not surprising that in the eastern United States %INPPFD for overcast conditions was the most appropriate predictor of %CPPD (LS and TS), and that for cloudless conditions the predictive models improved with increasing haze, or diffuse light levels.

In climates with predominantly clear conditions throughout the growing season, direct light, or sunflecks, may contribute a relatively greater percentage of the total light accumulated at canopy positions throughout the season, and much attention has been devoted to the study of the importance of sunflecks within forest

communities (Anderson, 1964a; Evans, 1956; Evans et al., 1960) and plant canopies (Lakso, 1980; Looney, 1968). On a clear day up to 80% of the radiant energy reaching a tropical rainforest floor was from sunflecks (Evans, 1956), and within an apple canopy, light levels were very low at interior positions throughout the day when sunflecks were excluded (Heinicke, 1966; Klein et al., 1991; Lakso and Musselman, 1976). Therefore, in areas with predominantly clear conditions during the growing season, sunflecks or direct light may constitute a larger proportion of the total available light within the canopy, and the relationship between %INPPFD and %CPPD could be different; %CPPD may be more closely related to %INPPFD measured for clear conditions.

Generally, instantaneous measurements from areas with predominantly clear conditions were made under cloudless conditions (Barritt et al., 1987; Morgan et al., 1984; Patten and Proebsting, 1986). However, based on detailed cumulative light measurements within apple canopies, and observations on tree growth patterns in an area with predominantly clear sky conditions during the growing season (British Columbia, Canada), Heinicke (1963) surmised that diffuse light may be a major contributor to the total cumulative light throughout the season. The uranyl oxalate measurement technique used by Heinicke (1963) to quantify light levels within the canopy has been severely criticized (Anderson, 1964a). Uranyl oxalate solutions are most sensitive to ultra violet and infrared radiation, and may not have represented physiologically active radiation levels. Additional research should be conducted in

locations with predominantly clear sky conditions to test the validity of instantaneous measurements under these conditions, and to develop new models.

Regardless of the prevalent weather conditions at a given location, it often may be necessary to make instantaneous measurements under cloudless conditions, and sunflecks should not be avoided. The importance of sunflecks in areas dominated by clear conditions has previously been discussed, and in areas with predominant overcast conditions the avoidance of sunflecks could lead to the underestimation of canopy light levels because diffuse light levels would be lower due to the reduced ambient diffuse light conditions of the clear day (Lakso and Musselman, 1976). Various methods have been used to account for sunflecks within plant canopies, including the line quantum sensor (Barritt et al., 1987), and other modified sensors that measure an increased surface area (Evans et al., 1960; Marini and Barden, 1982). More precise predictions may result from instruments that measure greater surface area than were possible with the silicon photocells in our study, particularly for clear conditions. Predictive models for instruments that measure greater surface area may need to be developed to clarify these relationships and predictive capabilities.

In light distribution studies under forest canopies, Anderson (1964c) found that light conditions often changed dramatically (clouds, haze) before completion of a series of instantaneous measurements, resulting in significant errors. A series of instantaneous measurements within a forest community could require 5 to 10 min for

completion due to the logistics of making measurements over a large area, and the difficulty in obtaining an ambient measurement. In our study, the series of instantaneous measurements was completed in less than 90 sec with the silicon photocell sensors; therefore, changes in ambient conditions were minimized. All measurements were made under relatively uniform light conditions, whether the conditions were overcast or cloudless. Variable conditions (partly cloudy) were avoided in this study due to the difficulty of accounting for the changing conditions. If the ambient light conditions do change significantly during a series of instantaneous measurements, the precision of predicted cumulative light levels would probably decrease, as was found with the quantum sensor measurements.

For both hazy and overcast conditions, the predictive models were equivalent for the two years evaluated in this study, although these years had quite different weather conditions during the growing season. Weather conditions were more cloudy and rainy in 1989 with total cumulative late-season PPD (July 22 to October 4) of 2,259 moles·m<sup>-2</sup>; in 1990 there was appreciably more cloud-free weather with total cumulative late-season PPD of 2,507 moles·m<sup>-2</sup>. This would be equivalent to about a week of additional available light over the final 10 weeks of the season in 1990. Weather conditions will of course vary from year-to-year for any given location, but the equivalence of the models between these two years strengthens the validity of these models.

The measurement and characterization of the canopy light environment is a complicated process, but we have demonstrated that instantaneous light measurements made with inexpensive silicon photocell and quantum sensors were reliable predictors of both late-season and total-season cumulative light levels within an apple canopy. These results support the validity of instantaneous measurements used in previous studies and allow for the comparison of results between studies. Instantaneous measurements can be made at any time of the season, given the correct model is used. However, after canopy development is complete, the 1-to-1 relationship between %INPPFD and %CPPD<sub>LS</sub> can be used for the remainder of the growing season. Instantaneous measurements do not require the equipment and computer facilities necessary for the direct measure of cumulative light levels.

Uniformly overcast conditions would be preferable for instantaneous measurements in the eastern United States, but the average of several instantaneous measurements made under hazy conditions will also yield relatively precise estimates of %CPPD. Assuming that instantaneous measurements are made rapidly, avoiding drastic changes in ambient light conditions, relative cumulative PPD levels (%) can be predicted and used to estimate the cumulative total quantum energy received at any canopy position by multiplying by the total incident PPD received at that location. Incident PPD can be measured directly, or sometimes these data are available from weather monitoring stations. Thus, the amount of quantum energy received at distinct canopy positions may be estimated.

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## Chapter IV

### Light Environment and Time of Harvest Affect 'Delicious' Apple Fruit

*Abstract.* Photosynthetic photon flux density (PPFD) was measured at multiple canopy positions throughout the growing season in 1989 and 1990 and used to explain variation in quality characteristics of 'Delicious' apples from these positions at 135, 145, 155, and 165 days after full bloom (DAFB). The number of hours above an average PPFD threshold of  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  ( $\text{HR}_{250}$ ) explained on the average about 2% more of the variation in fruit quality characteristics than other PPFD threshold levels or total cumulative photosynthetic photon density (PPD) in each year. Fruit red color had a positive linear relationship with  $\text{HR}_{250}$  on all harvest dates in both years; intercepts increased on each successive harvest date. The slopes and  $R^2$  were greatest at 135 DAFB, and decreased on each successive harvest date. Intensity of red color (A/B ratio) and soluble solids concentration also increased linearly with  $\text{HR}_{250}$ , with equivalent slopes and increasing intercepts on each successive harvest date. Fruit weight, flesh firmness, length/diameter ratio, and starch index were not consistently affected by any measure of canopy light levels. Except for intensity of red color, relationships developed between fruit quality characteristics and cumulative late-season PPD during the final 10 weeks before harvest ( $\text{CPPD}_{\text{LS}}$ ) had similar trends compared to the models for  $\text{HR}_{250}$  on all dates in both years. Relationships between fruit quality characteristics and  $\text{CPPD}_{\text{LS}}$

estimated from instantaneous PPFD measurements yielded models comparable to those developed for the more detailed cumulative light measurements.

## Introduction

Previous studies have reported that light environment influences apple fruit quality at harvest, including red color, soluble solids concentration, and fruit size. However, these data are largely the result of studies involving imposed shade treatments to achieve desired ranges in light levels (Doud and Ferree, 1980; Jackson and Palmer, 1977; Marini et al., 1991; Patten and Proebsting, 1986; Robinson et al., 1983; Seeley et al., 1980). While these studies illustrate some of the basic relationships between fruit quality and light levels, imposed shade treatments do not accurately represent the natural shading conditions within a plant canopy because the shade treatments are generally applied to whole trees or limbs, and not just the immediate vicinity of the fruit. The influence of the natural canopy light environment on fruit quality has been investigated, but the majority of these studies were conducted in arid climates with predominantly cloudless conditions prevalent during the growing season (Heinicke, 1966; Barritt et al., 1987; Morgan et al., 1984; Patten and Proebsting, 1986; Southwick et al., 1990). Due to the prevalent cloudless conditions, relative diffuse light levels would be lower in these regions compared to humid regions, such as the eastern United States (Heinicke, 1967). Light availability within the tree canopy may differ between arid and humid regions due to the differences in diffuse light levels (Lakso and Musselman, 1976). Therefore, relationships between fruit quality characteristics and light levels developed in arid regions may not be directly applicable to humid regions.

With the trend for higher-density apple orchards there is a need for additional information on the influence of canopy light levels on fruit quality. Programmable dataloggers and inexpensive silicon photocell sensors provide an inexpensive method to quantify light levels at many specific canopy positions throughout the growing season, and unlike the integrative methods used by Heinicke (1963), these measurements are not confounded by spectral changes within the canopy because the silicon photocell sensors measure only photosynthetically active radiation. In addition, through the use of high-speed computers, the light measurements from these specific canopy positions can be expressed in a variety of ways (not just cumulative totals) for comparison with fruit quality measurements.

The objectives of this study were to use detailed light measurements from multiple canopy positions (representing a range of light levels) to explain the variation in apple fruit quality characteristics at each position, and to determine how harvest date interacts with these relationships. A second experiment was conducted to validate and compare the use of estimated light levels derived from instantaneous measurements to explain variation in fruit quality characteristics of fruit from different canopy positions.

### **Materials and Methods**

*Orchard.* The study was conducted with fifteen-year-old 'Red Prince Delicious'/MM.111 trees growing on the Virginia Polytechnic Institute and State

Univ. Horticulture Farm, Blacksburg, VA. Rows were oriented in an E-W direction, with an in-row and between-row spacing of 5.5 and 6.1 m, respectively. Average tree height and width were 5.4 and 4.8 m, respectively, with an average trunk circumference of 60 cm. Yield efficiency in both years was reduced by spring frost, and was 0.82 and 0.68 kg / cm<sup>2</sup> trunk cross-sectional area in 1989 and 1990, respectively. Full bloom for both years was on 20 April.

***Light sensor construction.*** Silicon photocell sensors were constructed according to the design of Grappadelli and Coston (1988) and are described in detail in Chapter III. These sensors consisted of a silicon photocell (Texas Optoelectronics Inc., Garland, TX), a selective glass filter excluding wavelengths above and below 400 to 700 nm (B638, Schott Optical Glass, Inc., Duryea, PA), a diffusive plexiglass top, and a clear plexiglass body covered in black-plastic electricians tape except for a 1×2 cm window directly above the filter and sensor. These sensors were previously shown to have a similar response to a quantum sensor (Model LI190SB, LI-COR, Lincoln, NE) when tested over a range of light levels (Grappadelli and Coston, 1988), and when tested under our field conditions in 1989 (data not presented). Sensors were connected to a Campbell Scientific 21X datalogger (Campbell Scientific, Inc., Logan, UT) through a 32-channel multiplexer (Campbell Scientific).

***Experiment 1.*** Twenty-two sensors were placed in close proximity to fruiting spurs within the canopy of a single 'Delicious' tree in 1989. Positions were chosen to provide a wide range of light levels; the sensors were not in a grid pattern. The

sensors were taped to furring strips which were nailed at varying heights onto five, 4.6 m-high, 5×10 cm wooden boards (3 to 5 sensors per board). The five boards were placed within the canopy of the tree, one within 50 cm of the trunk, and the remaining four in either the NE, NW, SE, or SW quadrants of the tree, respectively, about 50 to 100 cm from the periphery of the canopy. All sensors were oriented towards the southern-side of the board to ensure there was no shading from the board itself. Sensors were periodically levelled. For incident photosynthetic photon flux density (PPFD) measurements and comparison of the two sensor types, one silicon photocell sensor and one quantum sensor (Model LI190SB) were placed side-by-side on a 4.6-m board in the row where two trees had been removed. The datalogger was programmed to scan each sensor and record PPFD every 10 sec. These values were then summed over 5-min periods to get a photosynthetic photon density (PPD) in quantum units ( $\text{moles}\cdot\text{m}^{-2}$ ). Measurements were made from 22 July to 4 October, 1989.

Fruit were harvested within 30 cm of each sensor on 135, 145, 155, and 165 days after full bloom (DAFB). One spur with a single fruit and one spur with two fruit were selected on each harvest date to provide three total fruit per position per date in 1989. Each fruit was weighed (FW) and length and diameter were measured for the determination of the length/diameter (L/D) ratio. The percent of the fruit surface colored red was visually evaluated. Flesh firmness was measured with an Effigi firmness tester fitted with a 7.9-mm plunger (Model FT 327; McCormick Fruit

Tech, Yakima, WA) on the green and the red side of the fruit and averaged for a single value. Soluble solids concentration (SSC) was measured with an Atago model N-1 hand-held refractometer (McCormick Fruit Tech). Fruit were cut in half and rated for starch content with a potassium iodide solution on a scale of 1 to 9 (immature to overmature) and the number of seeds was recorded. Water core was evaluated on a scale of 1 to 8 (none to severe) and the presence of moldy core was noted.

In 1990, 15 sensors were placed in the same manner within the canopies of two trees (30 total sensors). The datalogger was programmed to record PPF<sub>D</sub> every 10 sec as in the previous year, but data were summed to 15-min PPD totals. Measurements were made for the entire growing season, from 23 March to 4 October, 1990. Fruit were hand-thinned to a single fruit per spur when they were 6 to 8 mm in diameter. Single fruit were not necessarily derived from the king bloom because spring frost had killed much of the king bloom. Fifteen fruit within 30 cm of each sensor were assigned a number from 1 to 15 according to their proximity to the sensor, and at 135, 145, 155, and 165 DAFB three fruit were randomly selected per sensor position. Fruit quality measurements were identical to those in 1989 except in addition to fruit red color, the intensity of red color (A/B ratio) was measured on the red side of each fruit with a Minolta Chroma meter model CR-200b (Minolta Corp., Ramsey, NJ).

**Experiment 2.** Six additional 'Delicious'/MM.111 trees were used in 1990. Five canopy positions were chosen per tree to yield a range of light levels for the development of regression relationships to explain variation in fruit quality. Position 1 was located at the top of the tree within 30 to 60 cm of the canopy periphery and within 50 cm of the central leader. Position 2 was located 150 to 200 cm below position 1. Position 3 was located at the interior of the canopy about 480 to 520 cm below position 1. Position 4 was located at the lower middle canopy at a height of about 150 cm above the ground and 150 to 200 cm from the canopy periphery. Position 5 was located on the canopy periphery at a height of about 150 cm above the ground. All five positions were in the S-W quadrant of the tree.

Five fruit were harvested from within 50 cm of each of the five canopy positions per tree at 135, 145, 155, and 165 DAFB. Therefore, a total of 30 fruit were harvested per position per date, and only spurs with single fruit were selected. Fruit quality measurements were the same as for experiment 1. PPF<sub>D</sub> was measured at each canopy position per tree per date on the first overcast day following each harvest (within 6 days) with a Lambda quantum sensor (Model LI-185, LI-COR, Lincoln, NB). Four measurements were made at each position, averaged, and divided by the incident PPF<sub>D</sub> measured next to each tree to calculate a proportion of the incident PPF<sub>D</sub>. These proportions were then multiplied by the cumulative late-season (22 July to harvest) PPD from the reference sensor used in experiment

1 (within 70 m of these trees) to estimate cumulative late-season PPD ( $CPPD_{LS}$ ) in quantum units ( $\text{moles}\cdot\text{m}^{-2}$ ).

*Statistical analysis.* Regression analysis (SAS, 1985) was used to relate fruit quality characteristics with PPF<sub>D</sub> measurements in experiment 1. Individual observations (fruit) rather than means of multiple fruit per sensor position were used to develop regression models. Cumulative late-season PPD measured from 22 July to harvest ( $CPPD_{LS}$ ), cumulative total-season PPD measured from 23 March to harvest ( $CPPD_{TS}$ ), and for FW cumulative early-season PPD measured from petal fall (PF) to PF + 45 days ( $CPPD_{ES}$ ) were used as regressor variables for explaining variation in fruit quality characteristics. Also, the number of hours above various average PPF<sub>D</sub> threshold levels were used as regressor variables by summing the number of five- or fifteen-minute (depending on year) time periods that averaged greater than some desired PPF<sub>D</sub> level. PPF<sub>D</sub> threshold levels of 100 to 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ , at 50  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  increments, were tested ( $HR_{100}$  to  $HR_{1000}$ ). In 1989 for FW, separate relationships were developed for the single and double fruit per spur as these were determined to be distinct populations ( $P < 0.05$ ). For experiment 2 in 1990, fruit quality characteristics were regressed against the estimated  $CPPD_{LS}$ . Models for both experiments were compared to each other with indicator (dummy) variables in multiple regression (Montgomery and Peck, 1982).

## Results and Discussion

*Expression of light levels.* Cumulative hours above an average PPFD threshold level of  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  ( $\text{HR}_{250}$ ) consistently explained an average of about 2% more of the variation in the fruit quality characteristics compared to all other measures of PPFD tested (Figs. 1 and 2 vs Tables 1 and 2). The use of threshold PPFD levels instead of cumulative PPD totals has biological relevance because physiological activities in apple trees including net photosynthesis (Barden, 1977) and red color development of the fruit (Saks et al., 1990) were shown to have threshold PPFD levels above which additional PPFD had no added effect. By using the amount of time above certain PPFD thresholds, equal weight was given to any PPFD level above the threshold. We tested average PPFD threshold levels of 100 to 1000  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  because we hypothesized that the threshold PPFD level could differ depending on the fruit quality characteristic being considered. Red color development had a low threshold PPFD level (Saks et al., 1990); whereas, SSC should presumably have a greater threshold due to its dependence on photosynthesis. However, the threshold level of  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  was superior for all fruit quality characteristics (data not presented).

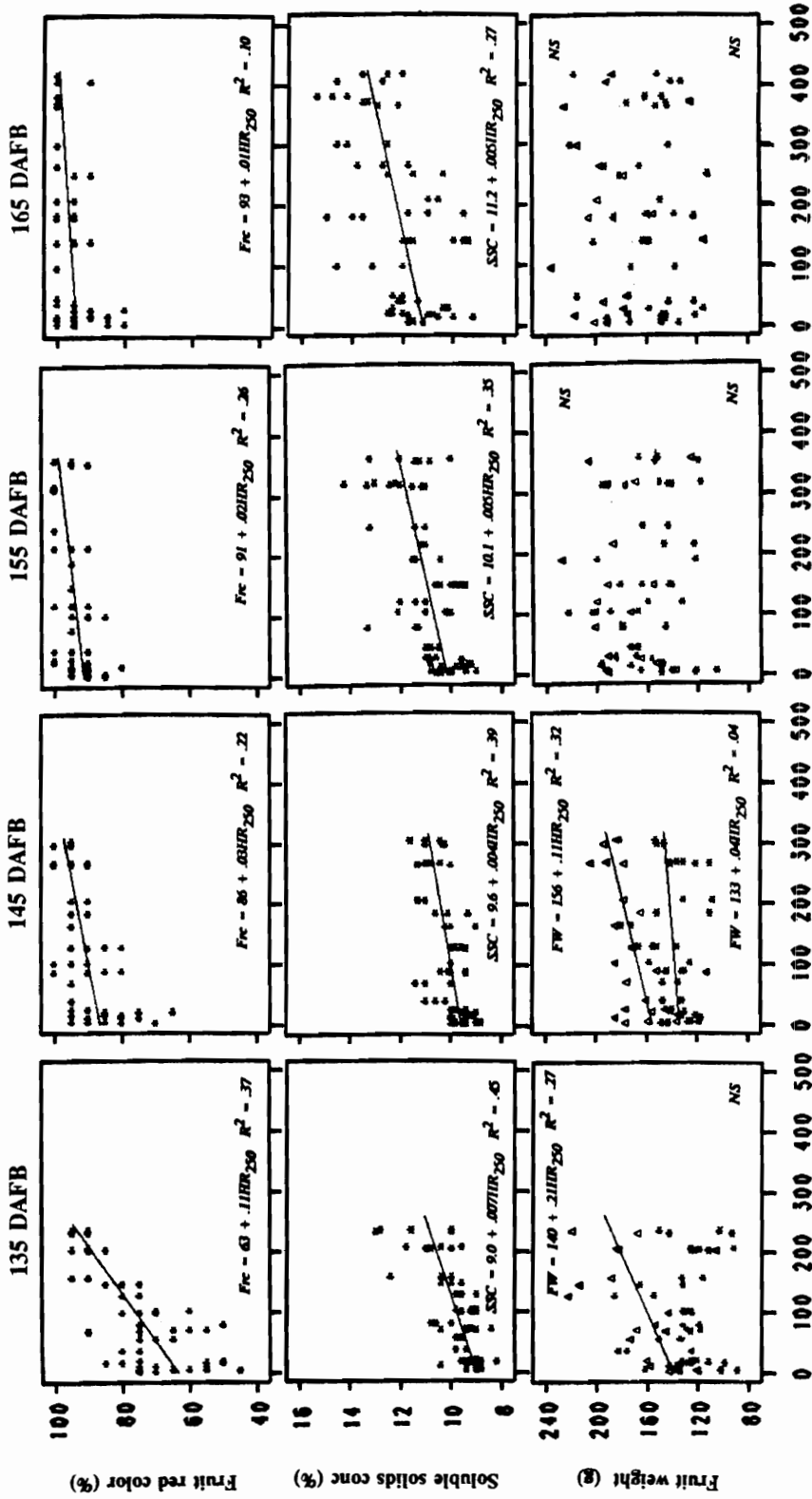
Among the cumulative PPD measures tested, models developed with  $\text{CPPD}_{\text{LS}}$  (Tables 1 and 2) explained as much or more of the variation in the fruit quality characteristics compared to the  $\text{CPPD}_{\text{TS}}$ , or  $\text{CPPD}_{\text{ES}}$  models (data not presented). Thus, cumulative PPD levels for the 10 weeks before harvest explained the greatest

amount of variation in the fruit quality characteristics. However, all of the measures used to quantify light levels within the canopy were closely correlated with each other; for example,  $HR_{250}$  and  $CPPD_{LS}$  had correlation coefficients of greater than 0.97 on all dates for both years. Therefore, differences in the amount of variation explained by each of the expressions of light were usually less than 5%.

Besides the work of Heinicke (1963; 1966), we are unaware of other studies where detailed light measurements for the entire growing season within an apple canopy were used to describe variation in fruit quality. The work of Heinicke (1963) was criticized because the uranyl oxalate technique used to quantify light levels within the canopy was responsive to ultra violet and infrared radiation and may not have represented photosynthetically or physiologically active radiation levels (Anderson, 1964). The silicon photocell sensors used in our study were not subject to such limitations due to the measurement of only photosynthetically active radiation.

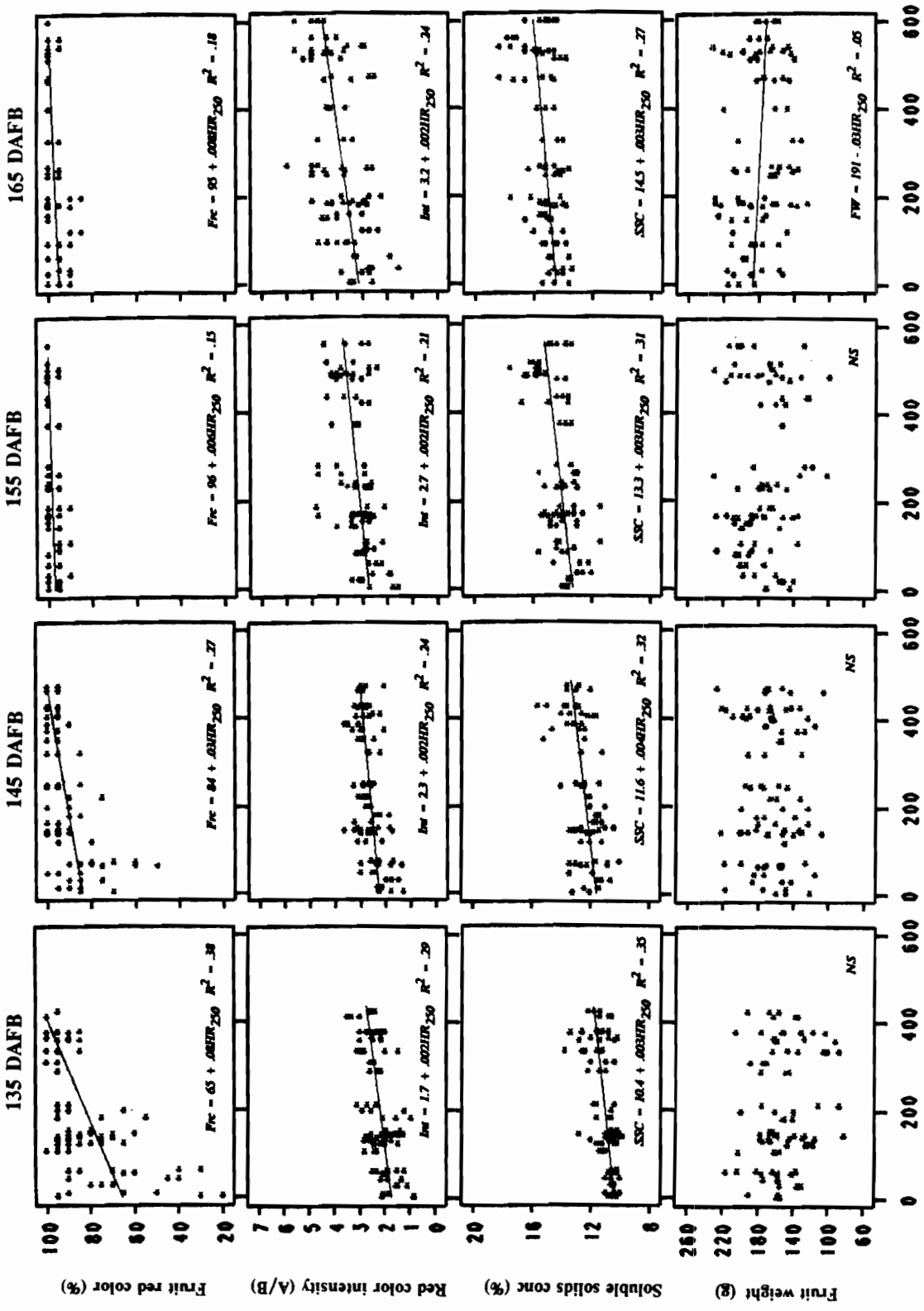
***Fruit red color.*** Fruit red color had a positive linear relationship with  $HR_{250}$  on all harvest dates in 1989 (Fig. 1) and in 1990 (Fig. 2). Models for 1990 had smaller slopes than in 1989, but due to the large amount of variation in the data there were no statistical differences. With each progressive harvest date within each year the models had greater intercepts and smaller slopes, and the  $R^2$  generally declined. At 135 DAFB in 1990, red color increased 1% for every 12 hours of average PPFD levels above  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  ( $HR_{250}$ ). By 145 DAFB in 1990,

**Fig. 1. Relationships between fruit red color (Frc), soluble solids concentration (SSC), and fruit weight (FW) and the number of hours above an average PPFD threshold level of  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  ( $\text{HR}_{250}$ ) for 'Delicious' fruit harvested on 135, 145, 155, and 165 days after full bloom (DAFB) in 1989. All regressions were significant at  $P < 0.05$  ( $n = 66$ ).**



Hours above an average PPFD threshold of 250  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  ( $\text{HR}_{250}$ )

Fig. 2. Relationship between fruit red color (Frc), red color intensity (Int), soluble solids concentration (SSC), and fruit weight (FW) and the number of hours above an average PFD threshold level of  $250 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  for 'Delicious' fruit harvested on 135, 145, 155, and 165 days after full bloom (DAFB) in 1990. All regression were significant at  $P < 0.05$  ( $n = 90$ ).



Hours above an average PPFD threshold of 250 μmol·m<sup>-2</sup>·sec<sup>-1</sup> (HR<sub>250</sub>)

it required 33 hours of  $HR_{250}$  for a 1% increase in fruit red color. By 155 and 165 DAFB intercepts reached a maximum value of about 92 and 95% red color for 1989 and 1990, respectively. The slopes were much smaller on these dates, particularly in 1990. One-hundred and twenty-five hours of  $HR_{250}$  were required for a 1% increase in the fruit red color by 165 DAFB in 1990. Compared to  $HR_{250}$ , the relationships between fruit red color and  $CPPD_{LS}$  were less consistent, with the smallest slope in 1989 on 145 DAFB (Table 1). Trends in the  $CPPD_{LS}$  models on the successive harvest dates in 1990 were similar to those for  $HR_{250}$  (Table 2).

Exponential (nonlinear) models were tested but showed no improvement over linear models (data not presented). For both years, no more than 38% of the variation in fruit red color was explained by  $HR_{250}$ , and the best relationships were for 135 DAFB. Multiple regression was performed with the stepwise procedure (SAS, 1985) using linear and quadratic terms of  $HR_{250}$  and SSC and an interaction term ( $HR_{250} * SSC$ ) to explain the variation in fruit red color. The model, Fruit red color (%) =  $-309 + 69 SSC - 3 SSC^2 + .0003 HR_{250}^2$  explained 51% of the variation in fruit red color on 135 DAFB in 1989. In 1990, the model, Fruit red color (%) =  $-185 + 24 SSC + .86 HR_{250} - .07 SSC * HR_{250}$  explained 52% of the variation in fruit red color. The additional variation in fruit red color explained by using multiple regressions with light and SSC terms was probably because SSC, in addition to its relationship with light level, is a precursor for anthocyanin in apple (Seigleman and Hendricks, 1958). Shading from spur leaves and adjacent fruit or branches probably

Table 1. Regression models for the relationship between fruit red color (Frc), soluble solids concentration (SSC), and fruit weight (FW) and cumulative late-season PPD levels in moles m<sup>-2</sup> (CPPD<sub>LS</sub>) for 'Delicious' in 1989.<sup>z</sup>

Fruit quality characteristic	Days after full bloom							
	135		145		155		165	
	Model	R <sup>2</sup>	Model	R <sup>2</sup>	Model	R <sup>2</sup>	Model	R <sup>2</sup>
Fruit red color	Frc = 63 + .02CPPD <sub>LS</sub>	.31	Frc = 85 + .009CPPD <sub>LS</sub>	.22	Frc = 91 + .005CPPD <sub>LS</sub>	.24	Frc = 94 + .004CPPD <sub>LS</sub>	.09
Soluble solids concentration	SSC = 8.9 + .002CPPD <sub>LS</sub>	.44	SSC = 9.5 + .001CPPD <sub>LS</sub>	.36	SSC = 10.0 + .001CPPD <sub>LS</sub>	.32	SSC = 11.1 + .001CPPD <sub>LS</sub>	.26
Fruit weight (Single)	FW = 137 + .047CPPD <sub>LS</sub>	.27	FW = 153 + .30CPPD <sub>LS</sub>	.34			NS	-
Fruit weight (double)	NS	-	Fw = 131 + .012CPPD <sub>LS</sub>	.09	NS		NS	-

<sup>z</sup> All models are significant at P < 0.05 (n = 66).

Table 2. Regression models for the relationship between fruit red color (Frc), intensity of red color (Int), soluble solids concentration (SSC), and fruit weight (FW) and cumulative late-season PPD levels in moles m<sup>-2</sup> (CPPD<sub>LS</sub>) for 'Delicious' in 1990.<sup>2</sup>

Fruit quality characteristic	Days after full bloom					
	135	145	155	165	Model	R <sup>2</sup>
Fruit red color	Frc = 63 + .03CPPD <sub>LS</sub>	Frc = 83 + .01CPPD <sub>LS</sub>	Frc = 97 + .002CPPD <sub>LS</sub>	Frc = 95 + .003CPPD <sub>LS</sub>		.16
Intensity of red color	Int = 1.6 + .001CPPD <sub>LS</sub>	Int = 2.2 + .0006CPPD <sub>LS</sub>	Int = 2.7 + .0007CPPD <sub>LS</sub>	Int = 3.0 + .0009CPPD <sub>LS</sub>		.24
Soluble solids concentration	SSC = 10.3 + .001CPPD <sub>LS</sub>	SSC = 11.5 + .001CPPD <sub>LS</sub>	SSC = 13.2 + .001CPPD <sub>LS</sub>	SSC = 14.3 + .001CPPD <sub>LS</sub>		.21
Fruit weight	NS	NS	NS	FW = 171 - .01CPPD <sub>LS</sub>		.04

<sup>2</sup> All models are significant at P < 0.05 (n = 90).

contributed to the unexplained variation in fruit red color. Temperature differences among the positions may also have influenced the fruit red color by influencing anthocyanin synthesis (Siegelman and Hendricks, 1958).

Suppression of red color by imposed-shade treatments has been well documented in 'Delicious' (Robinson et al., 1983; Seeley et al., 1980) and other apple cultivars (Proctor and Creasy, 1971; Proctor and Loughheed, 1976). Heinicke (1966) reported that fruit red color development was closely related to the light levels in the immediate vicinity of 'Turner Delicious' fruit within the canopy. The best red color developed when fruit were exposed to greater than 70% full sun (FS), with adequate color development between 40 to 70% FS, and inadequate color development below 40% FS. Log functions were used to fit relationships between fruit color development and light levels in apple (Morgan et al., 1984) and sweet cherry (Patten and Proebsting, 1986) canopies; the log functions dictated a marked decrease in fruit color below about 10-15% FS. Our data showed wide variation in red color at light levels below 20 to 30% of incident, with the poorest-colored fruit but also highly-colored fruit present at these positions.

Differences in coloring potential among 'Delicious' strains may explain why Barritt et al. (1987) reported no correlation between light level and fruit red color of 'Oregon Spur Delicious', while light level was related to fruit red color of 'Turner Delicious' (Heinicke, 1966) and 'Red Prince Delicious' in our study. Most recently-planted 'Delicious' orchards in Virginia are of high-coloring 'Delicious' strains, but

there is still significant 'Delicious' acreage in the region of relatively low-coloring strains (Marini, personal communication). Harvest date clearly influenced the importance light levels on fruit red color. Even fruit at the lowest light levels within our canopy developed about 90% red color by 155 and 165 DAFB. For our conditions, 145 to 155 DAFB would probably be optimal for long-term storage of 'Red Prince Delicious'.

Intensity of red color also had a positive linear relationship with  $HR_{250}$  in 1990 (Fig. 2). Intercepts were greater on each successive harvest date, but the slopes were equivalent for all of the harvest dates. Therefore, even though the relationship between fruit red color and  $HR_{250}$  weakened and had progressively smaller slopes on the latter harvest dates, the relationship between intensity of red color and  $HR_{250}$  remained consistent through 165 DAFB. However, when intensity of red color was regressed against  $CPPD_{LS}$  the trend was similar to that found with fruit red color, where the slopes became progressively smaller on the successive harvest dates (Table 2). This was the only instance where the expression of light ( $HR_{250}$  vs  $CPPD_{LS}$ ) consistently altered the overall trend in models for the four harvest dates. Colorimeter measurements of 'Delicious' strains (A/B ratios) were related to visual rating of fruit color (Singha et al., 1991), and because the relationships ( $HR_{250}$ ) were more consistent over a longer harvest interval, A/B ratios may be better indicators of incident light levels than fruit red color. High-coloring 'Delicious' strains may not respond in the same manner as the moderate-coloring 'Red Prince Delicious'.

***Soluble solids concentration.*** SSC had a positive linear relationship with  $HR_{250}$  in both years on all harvest dates. Intercepts increased on each successive harvest in both years, and in 1990 SSC (intercepts) were greater than in 1989 (Figs. 1 and 2). In 1989 there was a greater slope on 135 DAFB, with equivalent slopes on 145, 155, and 165 DAFB. Slopes were equivalent on the four harvest dates in 1990. Therefore, unlike fruit red color, additional  $HR_{250}$  resulted in similar relative increases in SSC on the successive harvest dates, although the minimum SSC level (intercept) increased.  $HR_{250}$  explained 45%, and 35% of the variation in SSC in 1989 and 1990, respectively, on 135 DAFB; variation increased (lower  $R^2$ 's) on subsequent harvest dates for both years. Positive linear relationships were also found for SSC and  $CPPD_{LS}$  on all dates in both years, with similar trends across all harvest dates to the  $HR_{250}$  relationships (Table 2).

Imposed-shade treatments suppressed SSC by up to 22% (Doud and Ferree, 1980; Robinson et al., 1983; Seeley et al., 1980). Imposed-shade treatments were applied to the entire tree, or scaffold branches; thus, in addition to shading the immediate vicinity of the fruit, shoot leaves were also shaded. The importance of the shoot leaves for the accumulation of SSC in the fruit within the canopy was demonstrated in summer pruning experiments with apple (Marini and Barden, 1982; Morgan et al., 1984). Therefore, shading in the immediate vicinity of the fruit may be partially compensated for by translocated assimilates from the better-exposed portions of the canopy (exterior shoot leaves), as was shown within peach canopies

(Marini et al., 1991). By shading the shoot leaves, the imposed-shading treatments probably enhanced the suppression in SSC.

Based on imposed-shading, Seeley et al. (1980) indicated that light levels capable of producing acceptable red color may not result in adequate SSC, particularly in high-coloring 'Delicious' strains. To the contrary, our results indicate that within the canopy of the 'Red Prince Delicious' trees, there was a greater suppression in fruit red color compared to SSC over the same range of light levels on the early harvests (135, 145 DAFB) (Fig. 1 and 2). By 155 and 165 DAFB, our results agreed more closely with the imposed-shade studies. The suppression of SSC within our canopies generally agreed with previous studies with apple (Barritt et al., 1987; Ferree, 1989; Heinicke, 1966). Suppression of SSC from the high to the low light levels based on the regression equations was about 11 to 15% in 1989, and 10 to 14% in 1990 on the four harvest dates.

**Fruit weight.** Fruit weight data were separated into spurs with single fruit and spurs with two fruit in 1989 (Fig. 1). The single fruit/spur data had a positive linear relationship with  $HR_{250}$  on 135 and 145 DAFB, with nonsignificant relationships at 155 and 165 DAFB. The double fruit/spur had a weak significant positive linear relationship on 145 DAFB, with all other dates insignificant. When the single and double fruit per spur data were pooled the relationship with light level was not significant on any harvest date (data not presented). In 1990, bias due to multiple fruit per spur was removed by hand-thinning the fruit at a diameter of 6 to 8 mm.

In 1990, there was no relationship between FW and  $HR_{250}$  on 135, 145, or 155 DAFB, and a weak negative linear relationship on 165 DAFB (Fig. 2). Seed number had a weak linear relationship with FW on most dates in both years ( $R^2 = 0.04$  to  $0.12$ ), but seed number was not related to light level (data not presented). When FW was regressed against  $CPPD_{LS}$  there was still no consistent indication of an influence on FW (Table 1 and 2).

Imposed-shade treatments (11% FS) applied to 'Cox' trees for the entire season (Jackson and Palmer, 1977) or to 'Delicious' scaffold limbs ( $< 5\%$  FS) from about 50 DAFB until harvest (Robinson et al., 1983; Seeley et al., 1980) suppressed apple FW by 66 and 30%, respectively. Eighty-five percent of the variation in FW was explained by light level when data for a single 'Delicious' tree was used (Seeley et al., 1980). The suppression of FW was the result of a reduction in both cell number and cell size (Jackson et al., 1977). Since cell division in apple occurs until about 45 DAFB (Westwood, 1978), and imposed-shade reduced cell number and size, we tested cumulative early-season (20 April to 5 June) PPD ( $CPPD_{ES}$ ) as a regressor variable for explaining the variation in FW, but the relationships were not significant (data not presented). Shading within the canopy may not have been severe enough during the early season to influence cell division, or there could have been compensation from other portions of the canopy. Marini et al. (1991) reported that FW was the quality characteristic of peach that was most influenced by translocated photosynthates from unshaded portions of the tree.

Fruit weight suppression in apple due to natural canopy shading has generally been less severe and more variable when compared to the results of imposed-shade studies (Heinicke, 1966; Morgan et al., 1984). Again, this is probably the result of compensation or the supply of photosynthates from the better-exposed portions of the canopy. Still, suppressions in FW of 27 and 31% were reported for prune (Southwick, et al., 1990) and 'Delicious' apple (Barritt et al., 1987), respectively, within the canopy. Light level explained about 12 and 35% of the variation in prune and apple FW, respectively. In contrast, our results indicated that within natural 15-year-old 'Delicious' canopies there was insufficient evidence to suggest consistent reductions in FW due to light level.

'Delicious' trees used in our study had relatively open canopies, and Jackson (1967) reported that the influence of light levels on 'Cox' FW was enhanced in dense canopies, presumably due to a reduction in light penetration. Yet, within dense 28-year-old 'Starkrimson Delicious' canopies in Virginia, FW was greater for the basal and middle compared to the terminal portion of lower scaffold limbs on two consecutive years (Marini and Sowers, 1991), and fruit from the lower two-thirds of 'Golden Delicious' canopies had a lower percentage of small fruit compared to the upper canopy, although light levels were lower at these positions (Ferree, 1989). A greater leaf-to-fruit ratio as a result of the reduced crop load for the interior canopy (Ferree, 1989) may have compensated for the reduction in light level.

Differences in the prevalent sky conditions between the arid conditions of the western United States (Barritt et al, 1987; Heinicke, 1966; Patten and Proebsting, 1986; Southwick et al., 1990), and the humid conditions in the eastern United States may have contributed to the discrepancy in FW results by influencing canopy light levels. Lakso and Musselman (1976) demonstrated that light levels were greater at interior positions of apple canopies for hazy and partly cloudy conditions compared to cloudless conditions due to increased diffuse light levels. Light (PPFD) levels at interior canopy positions of prune (Southwick et al., 1990) and walnut (Klein et al., 1991) canopies in California averaged about  $30 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  or lower for cloudless conditions, but light levels at interior positions of our 'Delicious' canopies averaged 40 to  $65 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  for hazy or partly-cloudy conditions. This comparison may be confounded by differences in tree size, canopy density, and pruning practices due to the different species considered.

***Flesh firmness.*** There was a weak indication of an increase in flesh firmness with increasing  $\text{HR}_{250}$  at 135 DAFB in 1990 (Firmness (N) =  $77.9 + .02\text{HR}_{250}$ ,  $R^2 = 0.11$ ), and on 165 DAFB (Firmness (N) =  $64.7 + .009\text{HR}_{250}$ ,  $R^2 = 0.16$ ). There was, however, no indication of an influence in 1989 or on any other harvest dates in 1990. Robinson et al. (1983) reported an 7% decrease in flesh firmness with 'Delicious' from 5% to 100% full sun and Barritt et al. (1987) reported that fruit from the bottom of the canopy were 4% firmer; these differences may have been due to the greater FW of the apples from the higher light levels. Seeley et al. (1980) and

Ferree (1989) reported no effect of imposed, or natural light environment (or canopy position), respectively, on flesh firmness.

*L/D ratio, starch rating, water core, moldy core.* L/D ratio was not influenced by any measure of light within the canopy in our study. Rom and Ferree (1984) reported increased L/D ratio on young greenhouse-grown 'Starkrimson Delicious' trees receiving 16% FS from budbreak to fruit set. Robinson et al. (1983) found a 1% increase in L/D ratio of 'Miller Sturdeespur Delicious' from 5 to 100% FS. Apparently, differences in light levels within the canopy were insufficient to influence L/D ratio under our conditions. Starch rating was not influenced by any measure of light within the canopy under our conditions. Seeley et al. (1980) reported an increase in the starch rating for fruit receiving greater light levels compared to shaded fruit, but Barritt et al. (1987) reported a lower starch rating for better-exposed fruit within a natural canopy. Neither the occurrence of water core or moldy core was related to light level.

*Experiment 2.* In this experiment, the regressor used to explain the fruit quality measurements was an estimate of the  $CPPD_{LS}$  based on the percentage value from instantaneous measurements on a single overcast day. The relationships between the estimates of  $CPPD_{LS}$  and the fruit quality characteristics on the four harvest dates (Table 3) were similar to the models from experiment 1. (Tables 1 and 2). Coefficients of determination were lower for the relationships with percent

Table 3. Regression models for the relationship between fruit red color (Frc), intensity of red color (Int), soluble solids concentration (SSC), and fruit weight (FW), and estimated cumulative late-season PPD levels in moles m<sup>-2</sup> (CPPD<sub>LS</sub>) for 'Delicious' in 1990.<sup>z</sup>

Fruit quality characteristic	Days after full bloom							
	135		145		155		165	
	Model	R <sup>2</sup>	Model	R <sup>2</sup>	Model	R <sup>2</sup>	Model	R <sup>2</sup>
Fruit red color	Frc = 61 + .03CPPD <sub>LS</sub>	.29	Frc = 83 + .01CPPD <sub>LS</sub>	.21	Frc = 97 + .001CPPD <sub>LS</sub>	.15	Frc = 96 + .001CPPD <sub>LS</sub>	.10
Intensity of red color	Int = 1.5 + .001CPPD <sub>LS</sub>	.29	Int = 2.2 + .0005CPPD <sub>LS</sub>	.20	Int = 2.8 + .0004CPPD <sub>LS</sub>	.15	Int = 3.1 + .0004CPPD <sub>LS</sub>	.13
Soluble solids concentration	SSC = 10.6 + .002CPPD <sub>LS</sub>	.33	SSC = 11.2 + .002CPPD <sub>LS</sub>	.29	SSC = 12.9 + .001CPPD <sub>LS</sub>	.32	SSC = 14.2 + .001CPPD <sub>LS</sub>	.22
Fruit weight	NS	-	NS	-	NS	-	NS	-

<sup>z</sup> All models are significant at P < 0.05 (n = 150).

and intensity of red color, but for SSC, the relationships based on estimated  $CPPD_{LS}$  values had higher  $R^2$  compared to the models from experiment 1. These data support the use of instantaneous light measurements for use in explaining variation in fruit quality. Instantaneous light measurements offer a great advantage in the saving of time and money, and computer manipulations involved with the more detailed light measurements of experiment 1. Cumulative light measurements explained some additional variation in the fruit quality characteristics, but the benefit of the increased information would have to be weighed against the added time and expense inherent with detailed measurements.

In conclusion, it is clear that percent and intensity of red color, and SSC of 'Delicious' fruit were influenced by the light environment in the immediate vicinity of the fruit, but FW was not consistently influenced by light level. Cumulative late-season PPD levels, and the number of hours above a PPF threshold of  $250 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$  were highly correlated; however, even with these detailed cumulative light measurements throughout the entire season, we could usually explain no more than 40% of the variation in fruit quality characteristics on the early harvest dates, and even less of the variation on the later harvest dates. Other factors besides light contributed nearly two-thirds of the variation in the fruit quality measures for our conditions.

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## Final Discussion

The present trend in apple production in Virginia (and the rest of the world) is for higher-density orchards designed to produce a quick return on the initial capital investment. As a result of the increased planting densities there are many questions and concerns about the influence of shading on leaf and fruit physiology. Yet, much of the information available on the influence of light environment on leaf and fruit physiology has been derived from imposed-shade studies or experiments conducted in arid climates. The results of these studies may not represent actual natural canopy light conditions, or they may not be directly applicable to the humid conditions in the eastern United States. My experiments were designed to investigate the influence of the natural canopy light environment on leaf and fruit physiology in a humid climate.

The gas exchange potential of the spur leaves within the canopy was closely related to the canopy light environment, as previously demonstrated by other researchers. However, differences were apparent even before the spur leaves were fully-expanded, indicating either an effect of early-season shading on gas exchange potential, or some carry-over effect from shading the previous year. This would be an interesting area of further research. Even though the gas exchange potential of the spur leaves was influenced very early in the season, nectar production was not affected by canopy position, light level, or even the presence of spur leaves on nongirdled spurs. Apparently, nectar production within an apple canopy is almost

exclusively dependent on translocated assimilates, and not on the presence of spur leaves.

One of the most exciting results of my research was the precision with which instantaneous light measurements predicted relative cumulative seasonal light levels within the canopy. The similarity of the predictive models for 1989 and 1990 strengthens the validity of the models. In humid climates the models I have presented could provide reliable estimates of cumulative light levels from instantaneous measurements. In arid climates the models may be different, or could have less predictive accuracy, and research should be conducted in such areas to test my models and to develop new models if necessary. The use of instantaneous measurements to estimate cumulative light levels is certainly of interest to many researchers due to the prohibitive cost, both in time and money, of cumulative light measurements. Our results demonstrated that instantaneous measurements can be used in fruit quality studies, with similar precision compared to cumulative measurements. Instantaneous measurements also offer an easy method for growers to assess light levels within the canopy.

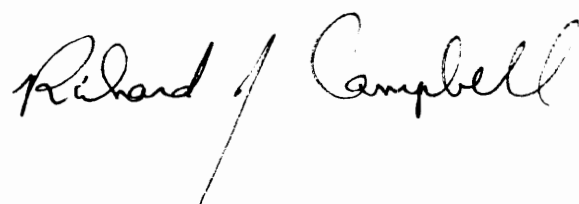
We are unaware of other studies within tree canopies which have made such detailed light measurements throughout the season for the development of relationships with fruit quality characteristics. It is disappointing that even with the detailed light measurements within the canopy, two-thirds of the variation in fruit quality was often still not explained by these measurements. Spur age, time of flower

opening or pollination, and other factors independent of light level may have contributed to variation in fruit quality. Certainly my results agree with much of the previous research relating light levels and fruit quality. However, previous studies (and conventional wisdom) have cited fruit weight as one of the fruit quality characteristics most sensitive to canopy light levels, but my results do not support these claims. Whether the conflicting data are the result of different prevalent sky conditions (arid vs humid), interpretation of data, or a combination of the two is not clear. However, based on my experiments, I believe that the influence of canopy light levels on fruit size has been over-emphasized for humid conditions. There would appear to be other factors of greater importance.

### **Vita**

Richard John Campbell was born on 18 August, 1964 in Homestead, Florida. He received his primary and secondary education in the Dade County Public School system. In the Fall of 1982 he entered the University of Florida where he received a Bachelor of Science in Fruit Crops in May 1986. He entered Virginia Polytechnic Institute and State University on a Presidential fellowship in 1986 and was granted his Master of Science degree in Horticulture in December 1988.

He continued his education at VPI&SU and was granted his Doctor of Philosophy degree in April 1991.

A handwritten signature in black ink that reads "Richard J. Campbell". The signature is written in a cursive style with a large, sweeping 'C' at the end.