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

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Abstract. **Light response curves for gas exchange characteristics were developed for spur leaves of 'Stayman' and 'Delicious' apple *(Malus domestica* Borkh.) from interior, intermediate, and exterior canopy positions throughout the season. At full bloom (FB), before full leaf expansion, exterior leaves had higher maximum rates of net photosynthesis (Pn), and a statistically different Pn light response curve than the interior leaves. Intermediate leaves had intermediate Pn rates and light response curves. Pn light response curves for all three 'Delicious' canopy positions differed from each other from FB + 6 weeks until the end of the season. Interior leaves had maximum Pn rates of only 50% to 60% of those for the exterior leaves from FB + 10 weeks until the end of the season. Light saturation levels were higher for the exterior leaves than for interior or intermediate leaves. Exterior leaves had a tendency throughout the season for higher quantum efficiency of Pn at subsaturating light levels than interior or intermediate leaves. Stomatal conductance was higher for the exterior than the interior or intermediate leaves of 'Delicious' on all dates. Water-use efficiency was equivalent among all leaves. Exterior leaves had higher specific leaf weight, dark respiration rates, and incident light levels on all dates than interior or intermediate leaves.**

Light environment influences leaf anatomy, morphology, and physiology among a wide range of plant species (Bazzaz and Carlson, 1982; Fails et al., 1982a, 1982b; Mahall and Schlesinger, 1982; Syvertsen, 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 major part 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 various canopy positions. Such information could influence pruning practices and could be useful for modelling whole-canopy gas exchange characteristics. The objective of this study was to develop light response curves for the gas exchange characteristics of apple spur leaves from interior, intermediate, and exterior canopy positions throughout the growing season.

Materials and Methods

Five 23-year-old 'Stayman'/MM.lll were used in 1989, and four 15-year-old 'Red Prince Delicious'/MM. 111 were used in 1990. All trees were located on the Virginia Polytechnic Institute and State Univ. Horticulture Farm, Blacksburg. '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 north–south with a 6. l-m in-row and 6. l-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 east–west with a 5.5-m in-row and a 6. l-m between-row spacing. At budbreak, four nonfruiting spurs in 1989 and eight 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 2nd-year wood as near to the periphery of the canopy as possible, intermediate spurs were selected ≈ 40 to 60 cm toward 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 four dates: FB, and FB + 2, 4, and 18 weeks; and for 'Delicious' in 1990 on eight dates: FB, and FB + 2, 4, 6, 10, 14, 18, and 22 weeks. Gas exchange characteristics were measured on one primary 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 (Barden et al., 1980). Pn was measured in an open system with an Anarad model AR-600 infrared gas analyzer (Anarad, Santa Barbara, Calif.). The leaf chamber was a modification of the one described by Syvertsen 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·s^{-1}, depending on leaf area. Air within the chamber was maintained at 28 ± 3C. Lighting was provided by 500R/3FL metal halide lamps (Westinghouse), and light levels were altered by covering the chambers with layers of neutral screening. Light levels of ≈ 0, 35, 150, 350, 500, 750, and 1150 µmol·m^{-2}·s^{-1} were used. Shading treatments were applied from least to most shade without randomization, as a preliminary experiment yielded equal

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Abbreviations: FB, full bloom; Pn, net photosynthesis; PPFD, photosynthetic photon flux density.

results for randomized and nonrandomized shading treatments. PPFD was measured at each shade level in the laboratory with a quantum sensor at the level of the leaf in the chamber. Following Pn measurements in the light, dark respiration was measured by turning off the lights and covering the chambers for 15 min. Carbon dioxide exchange 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_2 concentrations could not be calculated because absolute concentration of CO_2 in the chamber was not recorded. Water-use efficiency (WUE) was calculated by dividing Pn by transpiration (from dew point measurements). Following gas exchange measurements, the leaves were removed and area was 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) calculated. Photosynthetic photon flux density was measured at each spur position within the 'Delicious' canopy with a LI-COR quantum sensor (Model LI-185) on the first overcast day following gas exchange measurements and expressed as a percentage of incident PPFD (%IPPFD).

Light response curves for Pn 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:

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

where S_{Pn} is the maximum Pn rate, and G is the rate of approach to maximum. Light response curves for g_s were fit to the data using three-parameter nonlinear regression because g_s data did not approach 0 at 0 PPFD, making the two-parameter nonlinear model statistically inferior for these data. The three-parameter equation is:

$$g_s = S_{gs} - (Y * e^{-G* PPFD})$$

where S_{gs} is the maximum g_s rate, G is the rate of approach to maximum, and Y 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 (a/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. PPFD levels for 95% saturation of Pn (light saturation point) were calculated for each position and date using the two equations above, but were not statistically compared.

Results

Differences in the Pn light response curves occurred at FB for spur leaves from the three 'Stayman' canopy positions (Table 1). The exterior leaves had higher S_{Pn} than the interior leaves; intermediate leaves had an intermediate S_{Pn}. On the remaining dates, FB + 2, 4, and 18 weeks, the exterior leaves had a higher S_{pn} and rate of approach to maximum (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 Pn light response curves of spur leaves from the three canopy positions (Table 2, Fig. 1). The exterior leaves had a higher S_{pn} and lower G than the interior leaves. The intermediate leaves had intermediate S_{Pn}. and G values. By FB + 2 and FB + 4 weeks, the interior and intermediate leaves had smaller S_{Pn} 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_{pn}. Interior and exterior leaves also had different G values, but G values were similar for the interior and intermediate leaves. Pseudo R^2 were ≥ 0.95 for all regression curves, demonstrating the excellent goodness of fit for the models to the data (Fig. 1).

Table 1. Regression coefficients for net photosynthetic ($\mu mol \cdot m^{-2} \cdot s^{-1}$) light response curves and light saturation levels of 'Stayman' leaves from interior, intermediate, and exterior canopy positions at four sampling dates.[z] Equation: $Pn = S_{Pn} * [1 - e^{(-G \cdot PPFD)}]$.

Canopy position	Photosynthetic regression coefficients S_{Pn}	G	Light saturation level[y]
	FB		
Interior	4.5 a	0.0042 a	713
Intermediate	6.5 ab	0.0040 a	748
Exterior	7.8 b	0.0033 a	908
	FB + 2 weeks		
Interior	14.2 a	0.0040 b	748
Intermediate	16.2 a	0.0039 b	768
Exterior	21.7 b	0.0032 a	936
	FB + 4 weeks		
Interior	15.5 a	0.0064 b	468
Intermediate	15.5 a	0.0056 b	534
Exterior	18.3 b	0.0037 a	810
	FB + 18 weeks		
Interior	8.6 a	0.0073 b	410
Intermediate	9.6 a	0.0061 b	491
Exterior	13.0 b	0.0040 a	748

[z] Coefficients within columns and dates followed by the same letter do not differ at an experimentwise error rate of 0.05 (n = 5). Coefficients were compared with indicator variables.

[y] PPFD level ($\mu mol \cdot m^{-2} \cdot s^{-1}$, where Pn was 95% of maximum.

Light saturation points for Pn were higher for the exterior leaves of both 'Stayman' and 'Delicious' on all dates (Tables 1 and 2; Fig. 1 for 'Delicious'). The lowest light saturation points for leaves at all positions were reached by FB + 14 or FB + 18 weeks with 'Delicious'. Exterior leaves appeared to have higher quantum efficiency at sub-saturating PPFD levels than leaves at the other positions (Fig. 1), but no statistical differences were found when linear equations were fit to the Pn data at PPFD levels < 200 $\mu mol \cdot m^{-2} \cdot s^{-1}$ for each position and compared with indicator variables.

Exterior leaves had higher maximum 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, Fig. 2). There was no difference in G or Y among the positions on these dates. By FB + 6 weeks, and for the remainder of the season, intermediate and exterior leaves had higher S_{gs} values than interior leaves, and G and Y remained equal among all three positions. Pseudo R^2 were ≥ 0.93 for the regression curves for all dates

Table 2. Regression coefficients for light response curves of net photosynthesis (μmol·m^{-2}·s^{-1}) and stomatal conductance (mmol·m^{-2}·s^{-1}), and light saturation levels of 'Delicious' leaves from interior, intermediate, and exterior canopy positions on eight sampling dates.' Equations: Pn = S_{Pn} * [1 – et-$^{(G·PPFD)}$]; g_S = S_{GS} – [Y – e($^{-G·}$PPFD)].

Canopy position	Photosynthetic regression coefficients		Light saturation level[y]	Stomatal conductance regression coefficients		
	S_{Pn}	G		S_{gs}	G	Y
			FB			
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
			FB + 2 weeks			
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
			FB + 4 weeks			
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
			FB + 6 weeks			
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
			FB + 10 weeks			
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
			FB + 14 weeks			
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
			FB + 18 weeks			
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
			FB + 22 weeks			
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

[z] Coefficients within columns and dates followed by the same letter do not differ at an experimentwise error rate of 0.05 (n = 4). Coefficients were compared with indicator variables.

[y] PPFD level (μmol·m^{-2}·s^{-1}) where Pn was 95% of maximum.

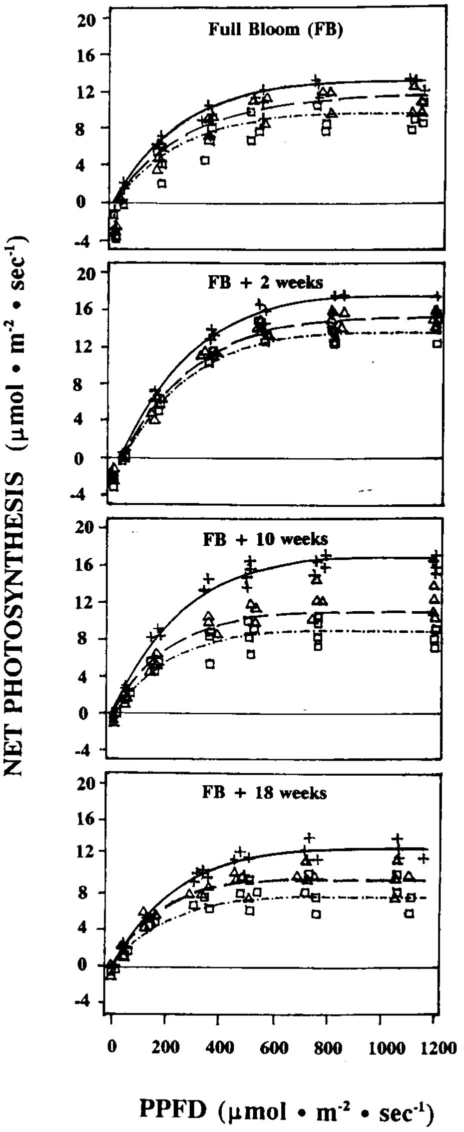

Fig. 1. Light response curves of 'Delicious' spur leaves for net photosynthesis measured at FB, FB + 2 weeks, FB + 10 weeks, and FB + 18 weeks. MacArthur–Wilson saturation equations represent the interior (□, - · - · -), intermediate (△, - - -), and exterior (+, ——) canopy positions. Equations (interior, intermediate, exterior): FB; Pn = 9.7 * [1 – e$^{(-0.0045*PPFD)}$], Pn = 11.9 * [1 – e$^{(-0.0041*PPFD)}$], Pn = 13.7 * [1 – e$^{(-0.0032*PPFD)}$]. FB + 2 weeks; Pn = 14.3 * [1 – e$^{(-0.0040*PPFD)}$], Pn = 15.4 * [1 – e$^{(-0.0036*PPFD)}$], Pn = 17.8 * [1 – e$^{(-0.0034*PPFD)}$]. FB + 10 weeks; Pn = 8.8 * [1 – e$^{(-0.0060*PPFD)}$], Pn = 11.1 * [1 – e$^{(-0.0049*PPFD)}$], Pn = 16.4 * [1 – e$^{(-0.0040*PPFD)}$]. FB + 18 weeks; Pn = 7.9 * [1 – e$^{(-0.0070*PPFD)}$], Pn = 9.4 * [1 – e$^{(-0.0064*PPFD)}$], Pn = 12.9 * [1 – e$^{(-0.0041*PPFD)}$].

and positions. Maximum WUE ranged from 3.2 to 5.7 μmol CO_2/mmol H_2O 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 IPPFD measured next to the spurs was highest at the exterior position on all dates (Table 3). The interior and intermediate positions did not statistically differ, although there was a trend for higher %IPPFD at the intermediate position on all dates. Percent IPPFD 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 (Table 3). Exterior leaves had higher SLW, and interior and intermediate leaves were statistically equivalent, although there was a trend for higher SLW at the intermediate position. SLW increased throughout the season for all of the positions. Dark respiration (Rd) was highest for the exterior leaves on all dates. After FB + 2 weeks, Rd tended to decrease for all three positions until FB + 18 weeks.

Discussion

Reductions in maximum Pn of 50% were reported for leaves of many species grown in low-light environments relative to those in full sun (Bazzaz and Carlson, 1982; Kappel and Flore,

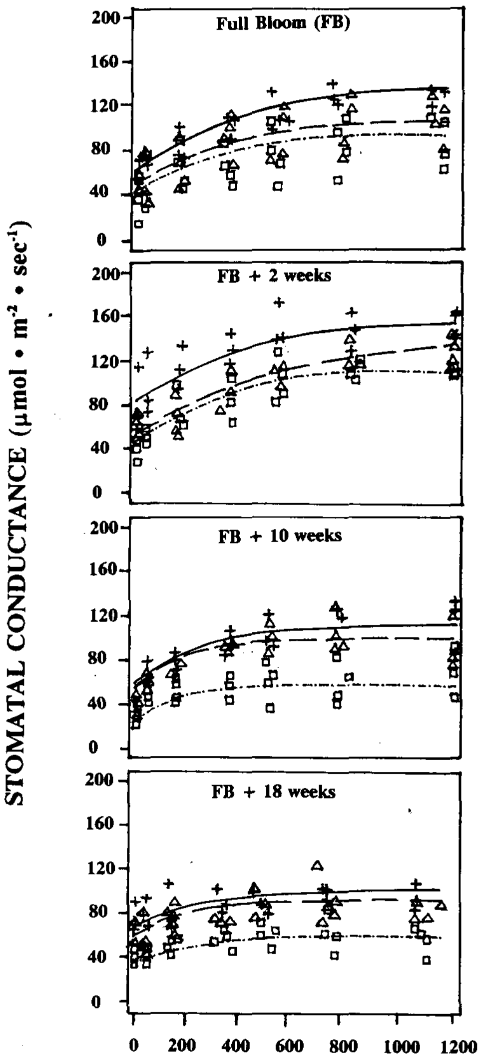

Fig. 2. Light response curves of ‘Delicious’ spur leaves for stomatal conductance (g_s) measured at FB, FB + 2 weeks, FB + 10 weeks, and FB + 18 weeks. McArthur–Wilson equilibrium equations represent the interior (□, - · - - · -), intermediate (△, - - -), and exterior (+, ——) canopy positions. Equations (interior, intermediate, exterior): FB; $g_s = 88 - [49 - e^{(-0.0032*PPFD)}]$, $g_s = 103 - [59 - e^{(-0.0050*PPFD)}]$, $g_s = 133 - [76 - e^{(-0.0025*PPFD)}]$. FB + 2 weeks; $g_s = 110 - [62 - e^{(-0.0043*PPFD)}]$, $g_s = 137 - [85 - e^{(-0.0020*PPFD)}]$, $g_s = 150 - [74 - e^{(-0.0035*PPFD)}]$. FB + 10 weeks; $g_s = 58 - [30 - e^{(-0.0150*PPFD)}]$, $g_s = 96 - [50 - e^{(-0.0100*PPFD)}]$, $g_s = 112 - [62 - e^{(-0.0046*PPFD)}]$. FB + 18 weeks; $g_s = 64 - [24 - e^{(-0.0052*PPFD)}]$, $g_s = 90 - [32 - e^{(-0.0064*PPFD)}]$, $g_s = 98 - [31 - e^{(-0.0046*PPFD)}]$.

Table 3. Percent incident PPFD (%IPPFD), specific leaf weight (SLW), and dark respiration (Rd) of ‘Delicious’ leaves from interior, intermediate, and exterior canopy positions.[z]

Canopy position	IPPFD (%)	SLW ($mg \cdot cm^{-2}$)	Rd ($\mu mol \cdot m^{-2} \cdot s^{-1}$)
		FB	
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
		FB + 2 weeks	
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
		FB + 4 weeks	
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
		FB + 6 weeks	
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
		FB + 10 weeks	
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
		FB + 14 weeks	
Interior	8 a	6.1 a	0.2 a
Intermediate	12 a	6.6 a	0.6 a
Exterior	60 b	9.7 b	1.2 b
		FB + 18 weeks	
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
		FB + 22 weeks	
Interior	7 a	6.1 a	0.4 a
Intermediate	11 a	6.9 a	0.7 a

[z] Means within columns and dates followed by the same letter do not differ at $P = 0.05$, by Tukey's HSD ($n = 4$).

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% of 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 ≈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* L. (Fails et al., 1982b), and peach *[Prunus persica* (L.) Batsch.] (Kappel and Flore, 1983). Within mature citrus (Syvertsen, 1984) and mango *(Mangifera indica* L.) (Schaffer and Gaye, 1989) canopies there were differences in Pn light response curves between interior and exterior leaves. Our Pn light response curves for the different canopy positions agree with these previous studies. Although maximum Pn (S_{Pn}) and rates of approach to maximum Pn (G) changed over the season, 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 difference may have been due to increased shading within the ‘Stayman’ trees because they were larger, although light levels were not measured to confirm this. This similarity in response 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; Syvertsen, 1984). Such methods yield no information about the rate of approach to maximum (G). For example, if the maximum Pn rates (S_{Pn}) 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 higher light levels found with quadratic equations. MacArthur-Wilson equations have the disadvantage of not fitting the Rd portion of the curve due to the limitations of the exponential equation, so light compensation points cannot be directly determined with these equations.

Enhanced quantum efficiency at subsaturating light levels was reported for leaves from low-light environments with citrus (Syvertsen, 1984), *F. benjamina* (Fails et al., 1982b), peach (Kappel and Flore, 1983), and *Fragaria vesca* L. (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 possibly higher quantum efficiency (nonsignificant trend) than the intermediate or interior leaves at all PPFD levels. In agreement with our results, Schaffer and Gaye (1989) reported that mango leaves in high light had higher quantum efficiency at subsaturating light levels than leaves in low light; 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 among plant species between leaves from low- and high-light environment.

Anatomical differences in leaves due to light environment probably contributed in part to the reductions in Pn potential of 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 higher 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 ($R^2 \geq 0.49$), 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).

Reductions in Pn potential could be due in part to a stomatal limitation to CO_2 diffusion (g_s), because the interior position had g_s rates only 50% to 70% of that for the exterior position. Reduced leaf conductance to water was reported for *F. benjamina* (Fails et al., 1982b) and chapparal shrub *(Ceanothus megaearpus* Nutt.) (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 *F. benjamina* (Fails et al., 1982a), and *Sinapis alba* (Wild and Wolf, 1980). Mahall and Schlesinger (1982) reported that WUE was higher for chaparral shrub leaves from a high-light environment, and this was also reported for citrus leaves (Syvertsen, 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 higher 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 statistically different Pn and g_s light response curves throughout the season. 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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