Light Intensity Influences Leaf Physiology and Plant Growth Characteristics of *Photinia* × *fraseri*

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Additional index words. fraser photinia, intercellular CO₂ concentration, net CO₂ assimilation, transpiration, stomatal conductance, relative leaf water content, specific leaf weight

Abstract. Leaf physiology and plant growth of *Photinia* × *fraseri* Dress were assessed when grown under full sunlight or (100% sun) or polypropylene shade cloth with a light transmittance of 69%, 47%, or 29% sun. Plants in 69% or 47% sun usually had the highest midday net CO₂ assimilation rates (A). Net CO₂ assimilation rate was most dependent on photosynthetic photon flux (PPF $R^2 = 0.60$), whereas stomatal conductance to water vapor was primarily influenced by vapor pressure deficit ($R^2 = 0.69$). Stomatal conductance was often inversely related to sun level, and intercellular CO₂ concentration was often elevated under 29% sun. Midday relative leaf water content and leaf water potential were unaffected by light regime. Light-saturated A was achieved at ≈ 1550 and $1150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ for 100% and 29% sun-grown plants, respectively. Under 29% sun, plants had a lower light compensation point and a higher A at PPF $< 1100 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Total growth was best under 100% sun in terms of growth index (GI) increase, total leaf area, number of leaves, and dry weight (total, stem, leaf, and root), although plants from all treatments had the same GI increase by the end of the experiment. Plants in all treatments had acceptable growth habit (upright and well branched); however, plants grown in 29% sun were too sparsely foliated to be considered marketable. There were no differences in growth among the four treatments 7 months after the *Photinia* were transplanted to the field.

Photinia × *fraseri*, commonly referred to as red tip or red top, is widely grown in nurseries in the southeastern United States and is widely popular among homeowners and landscape architects as a hedge plant. While *Photinia* is grown and primarily used in full sun, it reportedly has some shade tolerance (Dirr, 1983; Odenwald and Turner, 1987).

Plant species that can 'tolerate varying degrees of shade undergo integrated morphological and physiological changes that allow the plant to efficiently use lower levels of light (Boardman, 1977; Smith, 1982). Shade-tolerant species tend to have lower light compensation and saturation points when grown under reduced light (Boardman, 1977; Collard et al., 1977; Perry et al., 1986). Many shade-tolerant plants adapt to low light intensity by producing leaves that are thinner and broader than sun-grown leaves and possess increased chlorophyll concentrations and altered chloroplast orientation (Boardman, 1977; Collard et al., 1977; Fails et al., 1982a, 1982b; Logan, 1970). Increased horizontal branching (Fails et al., 1982a; Kappel and Flore, 1983) and a more open canopy (Fails et al., 1982a) are other means by which shade-grown plants improve light-harvesting capacity.

While it appears that *Photinia* × *fraseri* grows well in full sun or light shade (Dirr, 1983; Odenwald and Turner, 1987), we are not aware of any studies that have quantified the adaptation of *Photinia* to light levels. Andersen et al. (1988) reported net photosynthetic rates of containerized *Photinia* grown in full sun. Other researchers have examined various aspects of production (Bonaminio and Blazich, 1983; Dirr, 1984).

Information regarding the sun/shade tolerance of *Photinia* × *fraseri* may prove beneficial to the nursery and landscape industries. Our objectives were to assess long-term leaf gas exchange, leaf chlorophyll concentrations, and growth characteristics of *Photinia* × *fraseri* grown under four light regimes.

Materials and Methods

1987 to 1989 Experiments

Plant material. Rooted liners of *Photinia* × *fraseri* were obtained from a local nursery. In Apr. 1987, plants were potted into 3.8-liter containers with a medium of 2 pine bark : 1 Canadian sphagnum peat : 1 sand (by volume). One cubic meter of medium was amended with 2.97 kg dolomite, 2.97 kg superphosphate, 889 g Micromax (12S-0.1B-0.5Cu-12Fe-2.5Mn-0.05 Mo-1Zn) (Grace-Sierra Crop Protection Co., Milpitas, Calif.), and 5.93 kg Osmocote 18N-2.64P-9.96K (18-6-12) (Grace-Sierra). Plants were placed in a shadehouse (69% sun transmittance) until the start of the experiment.

A 24.4 × 17.1 × 2.0-m open-sided structure was constructed with the longitudinal axis oriented in a north-south direction. The structure was divided into four rows (i.e., four blocks) in a north-south direction. Each block consisted of four individual 6.1 × 4.3-m structures that transmitted light intensities at 100%, 69%, 47%, or 29% of full sun. Light intensity was modified by black woven polypropylene shade cloth (Chicopee, Gainesville, Ga.). The shade cloth served as a neutral filter (Yates, 1986). On 17 June 1987, four plants were placed 1 m above the ground on benches (2.7 × 0.8 m) centered below each of the four replicates of each of the four shade treatments. Azimuth angle of the sun was used to determine shade cloth size and bench height so as to minimize plant exposure to adjacent treatments and full sunlight during early morning and late afternoon (Buffington et al., 1981). Plants were top-dressed with 9.8 g Nutricote 16N-4.4P-8.3K (Type 180) (Plantco, Bramalea, Ont.) at the start of the experiment and then at 3-month intervals with Osmocote 18N-2.64P-9.96K (14 g/3.8-liter pot; 50 g/11.4-liter pot). On 9 Sept. 1987, plants were repotted in 11.4-liter containers in the same medium. One liter of water

Received for publication 10 Oct. 1990. This is Florida Agricultural Station Series no. R-01055. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Abbreviations: A, net CO₂ assimilation; Ci, intercellular CO₂ concentration; E, transpiration rate; GI, growth index; gs, stomatal conductance; LT, leaf temperature; PE, pretreatment expanded; PPF, photosynthetic photon flux RE, recently expanded; RLWC, relative leaf water content; SLW, specific leaf weight; VPD, vapor pressure deficit; WUE, water use efficiency.

was applied to each container daily at 0800 and 1400 HR via trickle irrigation. Two liters of water were applied daily at 0800 and 1400 HR to plants in 11.4-liter containers.

Leaf gas exchange. Carbon dioxide and H₂O exchange were monitored with portable, open-system instrumentation. Ambient and leaf chamber CO₂ and H₂O vapor concentration, air temperature, relative humidity, and PPF were measured with a Model LCA-2 infrared gas analyzer [Analytical Development Corp. (ADC), Hoddesdon, Herts, England], an air supply unit (flow rate 400 cm³/inch), and a Parkinson broadleaf chamber (aperture size = 6.25 cm²) (ADC). Boundary layer conductance was estimated according to Parkinson (1984), and the gas analyzer response to H₂O vapor was calculated according to von Caemmerer and Farquhar (1981). The A, stomatal conductance to H₂O vapor (g_s), transpiration rate (E), leaf temperature (LT), leaf-to-air vapor pressure deficit (VPD), and intercellular CO₂ concentration (C_i) were calculated using an ADC Model DL2 datalogger and the accompanying software. Water use efficiency (WUE) was estimated as the mole fraction of CO₂ uptake and H₂O vapor loss × 1000.

Gas exchange of fully expanded leaves oriented perpendicular to the sunlight and inserted into a leaf chamber was measured between 1000 and 1400 HR on selected days (19, 28, and 29 June 1987; 10 and 28 July 1987; 15 Sept. 1987; 21 Sept. 1988). Measurements were made on sunny days, except for 19 and 29 June, when the sky was partly and mostly cloudy, respectively. About 1 min was needed to approach steady-state conditions in the chamber. Two types of leaves were measured: fully expanded before treatment initiation [pretreatment-expanded (PE) leaves] and fully expanded after treatment initiation [recently expanded (RE) leaves]. One or two leaves of each age class in each replicate were measured. Before 28 July 1987, PE leaves were measured; on 28 July and 15 Sept., leaves of both age classes were measured; after 15 Sept. 1987, measurements were performed on RE leaves. Leaf gas exchange data derived from the two leaf age classes (28 July and 15 Sept.) are not presented separately because leaf age effects were not significant.

Data were subjected to analysis of variance using general linear model (GLM) procedures (SAS Institute, 1985) with light transmittance of shade cloth as the independent variable. Data were analyzed separately for each date of measurement. Linear and quadratic components were assessed for significance at $P = 0.05, 0.01, \text{ or } 0.001$. The A and g_s were also analyzed as a function of environmental variables (PPF, VPD, LT) by nonlinear regression procedures (Eisensmith, 1987). The relationship of A and g_s was also determined.

Leaf chlorophyll and growth characteristics. Chlorophyll concentration was quantified on 26 Aug. 1987 in disks of PE and RE leaves obtained from one plant per treatment per block. Three 1-cm leaf disks were immersed in N, N-dimethylformamide (DMF) for 24 h in the dark. Total chlorophyll, chlorophyll a, and chlorophyll b were quantified from absorbance at 647 and 664 nm (Inskeep and Bloom, 1985). Relative leaf water content, defined as: $\text{RLWC} = \frac{\text{stress weight} - \text{dry weight}}{\text{turgid weight} - \text{dry weight}} \times 100$ was also determined for PE and RE leaves on 26 Aug. Stress weight was the initial fresh weight, and turgid weight was the leaf fresh weight in the dark at near 100% relative humidity after the petioles of leaves had been immersed in water for 24 h.

Growth index, determined during June and Dec. 1987, and Nov. 1988 for all plants, was calculated as: $\text{GI} = (\text{height} + \text{width})/2$, where height and width were measured at their most extensive points. Shoot (stem + leaves) and root dry weights,

shoot : root ratio, number of leaves total and average leaf dry weight, total and average leaf area, and specific leaf weight, defined as $\text{SLW} = \text{leaf dry weight}/\text{leaf area}$, were measured on 20 Dec. 1987 (one plant per treatment per block) and 21 to 27 Dec. 1988 (two plants per treatment per block). The remaining plants were transplanted to the field [Dothan loamy sand (Plinthic paleudults) containing $\approx 1\%$ organic matter] for long-term evaluation under landscape conditions. GI was calculated during July 1989.

Data were analyzed by GLM procedures (SAS Institute, 1985). Linear and quadratic models were assessed for significance. Relative leaf water content was analyzed after square-root transformation (Gomez and Gomez, 1984).

1990 Experiments

Plant material. Two-year-old *Photinia × fraseri* obtained from a local nursery were repotted in 13.3-liter containers using the medium described above. Four plants were placed in 100% or 29% sun on 6 Apr. 1990.

Leaf gas exchange. Light response curves were compiled on 30 May using RE leaves of 100% and 29% sun-grown plants. PPF was manipulated by shading leaves with shade cloth. The A was monitored as a function of PPF for leaves of four sun- and shade-grown plants. Data were analyzed using nonlinear regression (Eisensmith, 1987). The light saturation points were then estimated as 95% of maximum A. Apparent quantum yields were estimated by using the slopes of the lines between 0 and 200 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. A t test was used to determine differences in dark respiration rate. Leaf gas exchange characteristics were also compiled for 100% and 29% sun-grown plants every 2 h from 0800 to 2000 HR on 31 May.

Leaf chlorophyll and leaf water potential. Chlorophyll content was measured on 20 June as previously described. Leaf water potential of the 100% and 29% sun-grown plants (four plants per treatment) was measured midday on 20 June using a pressure chamber apparatus (PMS Instrument Co., Corvallis, Ore.) (Scholander et al., 1965). Data were subjected to analysis of variance, and significant differences were assessed by a t test.

Results

1987 to 1989 Experiments

PPF, measured hourly at plant height on 29 Sept. from 0800 to 1900 HR in the 100%, 69%, 47%, and 29% sun treatments, indicated that the shade cloth ratings claimed by the manufacturer were accurate (results not shown). During midday, an average of $\approx 96\%$ of the variation in PPF was due to the shade cloth (Table 1), except on 29 June 1987, when cloudiness precluded consistent light conditions.

The A on sunny days was generally higher under 69% and 47% sun than under 100% or 29% sun (Table 1; see quadratic relationships). On average, A was highest under 69% sun. Plants in 29% sun tended to have lower A than plants exposed to higher light levels. The relatively low A of plants in 100% sun on 15 Sept. 1987 may have been due to moisture stress resulting from transplanting on 9 Sept. Of the independent variables (PPF, VPD, and LT), A was most dependent on PPF ($R^2 = 0.60$) (Fig. 1a); however, A was poorly correlated to VPD ($R^2 = 0.16$) and g_s ($R^2 = 0.13$) (results not shown).

The g_s often was inversely related to light regime (Table 1), although analysis of combined data indicated that PPF was poorly

Table 1. Midday (1000-1400 HR) leaf gas exchange characteristics of *Photinia × fraseri* grown under four levels of exposure to sunlight on selected dates during 1987 and 1988. Treatments were initiated 17 June 1987.

Characteristic and exposure to sun (%)	Date/leaf age ^z						
	19 June 1987	28 June 1987	29 June 1987	10 July 1987	28 July 1987	15 Sept. 1987	21 Sept. 1988
	PE leaves	PE leaves	PE leaves	PE leaves	PE + RE leaves	PE + RE leaves	RE leaves
PPF ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)							
100	1606	2069	655	2025	2008	2223	1976
69	1101	1477	381	1344	1367	1529	1331
47	623	1040	379	1018	963	1036	932
29	375	611	199	556	552	574	499
Significance	L***	L***	L**	L***	L***	L***	L***
R ²	0.921	0.972	0.719	0.950	0.938	0.980	0.984
A ($\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)							
100	10.6	10.8	8.3	12.9	8.9	6.0	12.0
69	12.7	11.2	5.0	11.9	10.7	9.4	14.4
47	10.5	10.5	6.7	11.3	10.6	9.5	10.4
29	7.1	8.7	3.1	8.4	8.2	8.1	8.2
Significance	NS	NS	Q**	L*	Q***	Q***	Q**
R ²	---	---	0.599	0.382	0.476	0.512	0.736
gs ($\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)							
100	244	210	269	280	247	170	163
69	317	220	226	262	277	235	195
47	361	198	324	324	332	283	202
29	296	202	271	262	307	271	208
Significance	L***	NS	Q*	NS	L*	L**	L**
R ²	0.528	---	0.380	NS	0.186	0.232	0.529
Ci ($\mu\text{mol}\cdot\text{mol}^{-1}$)							
100	223	208	251	218	231	239	174
69	228	207	273	220	223	222	168
47	253	208	273	237	237	233	211
29	267	227	297	250	253	244	235
Significance	L**	NS	Q*	L***	Q***	NS	L***
R ²	0.347	---	0.696	0.692	0.557	---	0.630

^zPE leaves fully expanded before treatment initiation; RE leaves fully expanded after treatment initiation. Leaf age effects were nonsignificant on 28 July and 15 Sept. 1987.

*, **, ***, NS Linear (L) or quadratic (Q) models significant at $P = 0.05, 0.01, \text{ or } 0.001$ or nonsignificant, respectively, based on F values.

correlated to gs ($R^2 = 0.11$; results not shown). VPD accounted for $\approx 70\%$ of the variation in gs (Fig. 1b). Transpiration rate (range = 5.0 to 7.8 $\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was seldom influenced by light regime. WUE (range = 0.9 to 2.5 $\text{mmol CO}_2/\text{mol H}_2\text{O}$) was often related to light regime, with lowest values occurring in 29% sun. Since A, but not E, was affected by light regime, changes in WUE (A/E) mirrored changes in A (results not shown). In addition, since light regime influenced A and gs, Ci was often affected by light regime, with higher Ci values often recorded under 29% sun (Table 1).

During 1987, increase in GI was inversely related to light regime (Table 2) due to increasing height with declining light level (results not shown). However, dry matter production (total, leaf, stem, and root), total leaf area, average area and dry weight per leaf, and RLWC were similar in all light regimes (Table 2). Plants under 69% and 47% sun produced the most

erage leaf area and shoot : root ratio, which increased with decreasing light. *Photinia* grown under 100% sun had the highest SLW, and total, leaf, stem, and root dry weights after two growing seasons; they also had the most leaves and total leaf area and thus were the most aesthetically appealing. Under 69% or 47% sun, dry matter and leaf production declined slightly, but these plants were of acceptable quality despite their more open appearance. The long-term response of plants grown under 29% sun was an open growth habit, reduced leaf production, and reduced total, shoot, and root dry weights (Table 2); we judged plant appearance to be unacceptable.

There were no differences in growth among the treatments 7 months after the *Photinia* were transplanted to the field (results not shown).

1990 Experiments

Fig. 1. Relationship of *Photinia × fraseri* (a) A to PPF undervarious levels of light, and (b) *gs* to leaf-to-air VPD. Measurements represent the combined midday data for 1987 and 1988.

Fig. 2. Light response curve for *Photinia × fraseri* leaves preconditioned to 100% (SNLV) or 29% exposure to sunlight (SHLV) from 6 Apr. to 31 May 1990. The A was measured on 31 May 1990 from 1000 to 1400 HR. Maximum PPF = $1881 \pm 8 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$; air temperature: SNLV = $28.4 \pm 0.2^\circ\text{C}$, SHLV = $28.9 \pm 0.1^\circ\text{C}$; leaf temperature: SNLV = $26.4 \pm 0.3^\circ\text{C}$, SHLV = $27.2 \pm 0.3^\circ\text{C}$; VPD: SNLV = $2.2 \pm 1.1 \text{ kPa}$, SHLV = 2.4 ± 0.1 .

sun-grown plants were higher than shade-grown plants throughout the day. WUE was higher in the full-sun regime during the early and late part of the day. The *gs* of plants under 100% sun was higher than shade-grown plants from 1600 to 2000 HR. Ci

Fig. 3. Diurnal characteristics of leaf gas exchange of *Photinia × fraseri* leaves preconditioned to 100% or 29% exposure to sunlight from 6 Apr. to 31 May 1990. Points and error bars represent the mean and ± 1 SE, respectively; $n = 4$. Leaf temperatures for 100% and 29% sun-grown plants, respectively, were as follows: 800 HR— 22.3 ± 0.2 , 21.9 ± 0.2 ; 1000 HR— 27.9 ± 0.3 , 25.9 ± 0.4 ; 1200 HR— 30.5 ± 0.4 , 29.2 ± 0.4 ; 1400 HR— 33.5 ± 0.8 , 30.0 ± 0.3 ; 1600 HR— 33.9 ± 0.5 , 31.4 ± 0.4 ; 1800 HR— 31.5 ± 0.2 .

was higher in 29%-sun leaves than in 100%-sun leaves. Leaf temperatures in 100% sun were 2 to 3°C higher during midday (see Fig. 3 legend).

The total chlorophyll concentration was higher in 29% than in 100% sun-grown plants, but the chlorophyll a : chlorophyll b ratio was higher in 100% sun-grown plants (Table 3). Midday leaf water potentials were not affected by light regime.

Discussion

Midday A of *Photinia* grown under 47% or 69% sun (Table 1; Fig. 1a) was generally higher than that of plants grown under 100% sun, although after two growing seasons, carbon gain was maximized in 100% sun (Table 2, see dry weights). The assessment of leaf gas exchange on exterior canopy leaves may have underestimated whole-plant A for sun-grown compared to shade-grown plants. Exterior canopy leaves in 100% sun received sufficient light to be operating near maximum A for most of the day (Figs. 2 and 3). Under 69% sun, exterior canopy leaves were exposed to light-saturating PPF only during midday

Table 2. Growth characteristics of and chlorophyll concentrations for *Photinia × fiaseti* under four levels of exposure to sunlight during 1987 and 1988. Treatments were initiated 17 June 1987.

Growth characteristic	Exposure to sun (%)				Significance	R ²
	100	69	47	29		
Increase in GI ^z (cm)						
June 1987–Dec. 1987	34	35	43	40	L**	0.22
Dec. 1987–Nov. 1988	84	83	74	72	L**	0.15
June 1987–Nov. 1988	118	116	118	112	---	---
Total dry wt (g)						
1987	69	100	108	95	---	---
1988	1221	1144	1074	720	L***	0.57
Total leaf dry wt (g)						
1987	21	30	29	26	---	---
1988	307	252	228	156	L***	0.78
Stem dry wt (g)						
1987	28	46	53	47	---	---
1988	662	659	635	432	L***	0.57
Root dry wt (g)						
1987	19	24	27	22	---	---
1988	252	234	210	132	L***	0.63
Shoot : root						
1987	2.58	3.20	3.17	3.28	---	---
1988	3.88	3.90	4.13	4.45	---	---
Leaf total (no.) ^y						
1987	82	120	123	98	Q*	0.40
1988	1005	834	711	519	L***	0.77
Total leaf area (1000 cm ²)						
1987	1.27	1.81	2.03	1.81	---	---
1988	16.6	14.4	13.5	10.2	L***	0.63
Area/leaf (cm ²)						
1987	16.2	15.2	16.6	18.6	---	---
1988	16.5	17.2	19.1	19.9	L***	0.51
Dry wt/leaf (g)						
1987	0.271	0.254	0.233	0.262	---	---
1988	0.306	0.301	0.324	0.304	---	---
Specific leaf wt (mg·cm ⁻²)						
1987	16.8	16.6	14.5	14.1	L*	0.27
1988	18.6	17.5	17.0	15.3	L***	0.65
Relative leaf water content* (%)						
RE leaf (1987)	92	92	94	94	---	---
PE leaf (1987)	94	93	94	93	---	---
Leaf chlorophyll concn* (µg·cm ⁻²)						
RE leaf (1987)	39.0	41.3	40.4	37.9	---	---
PE leaf (1987)	49.2	55.5	66.5	63.3	L***	0.70
Chl a : Chl b						
RE leaf (1987)	2.6	2.6	2.9	2.6	---	---
PE leaf (1987)	2.6	2.4	2.4	2.4	L*	0.25

^zIncrease in GI = (height + width)/2.

^yLeaf total, total leaf area, area/leaf, dry weight/leaf, and specific leaf weight were determined from all leaves harvested.

*Relative leaf water content and leaf chlorophyll concentration were measured on RE and PE leaves.

* ** * ***, ^{NS}Linear (L) or quadratic (Q) models significant at $P = 0.05$, 0.01 , or 0.001 or nonsignificant, respectively, based on F values.

Table 3. Leaf water potential, leaf chlorophyll concentration, and chlorophyll a : chlorophyll b ratio of *Photinia × fraseri* grown under 100% or 29% exposure to sunlight for 45 days. Measurements were performed 20 June 1990.

Characteristic	Exposure to sunlight (%)	
	100	29
Water potential ¹ (MPa)	- 0.88	- 1.00 ^{NS}
Chlorophyll concn (μg·cm ⁻²)	37.2	56.4***
Chl a : chl b	2.82	2.52***

¹Measurements were performed on leaves that were expanded after treatment initiation.

***, ^{NS}Significant at $P = 0.01$ or nonsignificant, respectively, by t test.

rophyll levels were similar in the 100% and 6970 sun regimes. Furthermore, light-saturated values of A were higher under 100% than 29% sun.

While the midday suppression in A under 100% sun may have been associated with partial stomatal closure, A and g_s appeared to be controlled by different environmental variables. The g_s was inversely related to VPD ($R^2 = 0.69$; Fig. 2b), similar to that reported for other species (Mooney et al., 1983; Schulze and Hall, 1982; Turner et al., 1984). However, A was primarily influenced by PPF ($R^2 = 0.60$), not VPD ($R^2 = 0.16$). Thus, A and g_s were not strongly coupled ($R^2 = 0.13$). In addition, the similar diurnal g_s of 100% and 29% sun-grown plants, but higher A of 100% sun-grown plants, resulted in a lower Ci and higher WUE (Fig. 3).

Photinia exhibited physiological and morphological adaptations to the various light regimes. Light-saturated A was achieved at =1500 and 1100 μmol·m⁻²·s⁻¹ for plants grown under 100% and 29% sun, respectively. Under 29% sun, plants had a lower light compensation point and a higher A at PPF less than =1100 μmol·m⁻²·s⁻¹. Although differences in light compensation occurred, there were no differences in other common shade adaptations, such as changes in apparent quantum yield and dark respiration rate (Boardman, 1977; Loach, 1967). Light-harvesting capacity was improved under shade through higher chlorophyll concentrations and the production of leaves that were broader and thinner than sun-exposed leaves. Plants growing in 29% sun also had a more open canopy than those in 100% sun, an adaptation that would improve light penetration to interior leaves (Fails et al., 1982a).

Morphological and physiological adaptations permitted *Photinia* growing under 69% or 47% sun to acclimate sufficiently, as evidenced by the relatively high rates of leaf gas exchange, total leaf area, and total, stem, root, and leaf dry weights. However, shade adaptations did not adequately compensate for other factors that may have limited A of 29%-sun plants, such as insufficient levels of carboxylating enzymes or a limited light-harvesting capacity (Boardman, 1977; Logan, 1970; Perchorowicz et al., 1981). Consequently, under 29% sun, the reduced A and total leaf area resulted in diminished total, shoot, root, and leaf dry weights (Table 3) by the end of 2 years of growth. The effect of reduced A under 29% sun, however, did not affect dry matter production in 1987. One interpretation is that mutual leaf shading became more important in shade than in sun plants with an increase in plant size.

Based on our results, *Photinia* might be classified as a facultative shade plant (Smith, 1982). Plants grown in 100% sun had the highest total, shoot, root, and leaf dry weights (Table 2) and were the most densely foliated, while plants grown under 47% and 69% sun acclimated without substantial reductions in

growth and total carbon gain. Plants grown under 29% sun exhibited reduced dry matter production and an unmarketable growth habit.

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