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

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**Abstract.** Leaf physiology and plant growth of *Photinia × fraseri* were assessed when grown under full sunlight or (100% sun) or polypropylene shadecloth 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 = 0.60), whereas stomatal conductance to water vapor was primarily influenced by vapor pressure deficit (R = 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 ≈ 1500 and 1150 μmol·m⁻²·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 μmol·m⁻²·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 comparable 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.

**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 superfosphate, 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) for the start of the experiment. A 24.4 × 17.1 × 2. O-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 shadecloth (Chicopee, Gainesville, Ga.). The shadecloth 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 shadecloth 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) (Plantec, 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

**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.

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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/min), 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 (gs), transpiration rate (E), leaf temperature (LT), leaf-to-air vapor pressure deficit (VPD), and intercellular CO₂ concentration (Ci) 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 shadecloth 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, or 0.001. The A and gs were also analyzed as a function of environmental variables (PPF, VPD, LT) by nonlinear regression procedures (Eisenmith, 1987). The relationship of A and gs 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 (Inskipe and Bloom, 1985). Relative leaf water content, defined as: RLWC = stress weight – dry weight / dry weight × 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: GI = (height + 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 leaf total and average leaf dry weight, total and average leaf area, and specific leaf weight, defined as SLW = leaf dry weight/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 paleultids) containing ≈ 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 shadecloth. The A was monitored as a function of PPF for leaves of four sun- and shade-grown plants. Data were analyzed using nonlinear regression (Eisenmith, 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 μmol·m⁻²·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

PFM, 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 shadecloth ratings claimed by the manufacturer were accurate (results not shown). During midday, an average of ≈ 96% of the variation in PPF was due to the shadecloth (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 (R² = 0.60) (Fig. 1a); however, A was poorly correlated to VPD (R² = 0.16) and gs (R² = 0.13) (results not shown).

The gs 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* | 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    |              |
| PPFD (μmol·m⁻²·s⁻¹)                   |               |              |              |              |              |              |              |              |
| 100                                   | 1606          | 2009         | 655          | 2025         | 2008          | 2223          | 19/16        |
| 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***          |              |
| R²                                    | 0.921         | 0.972        | 0.719        | 0.950        | 0.938         | 0.980         | 0.984        |
| A (μmol·m⁻²·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***          |              |
| R²                                    | --            | --           | 0.599        | 0.382        | 0.476         | 0.512         | 0.736        |
| gs (mmol·m⁻²·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**           |              |
| R²                                    | 0.528         | --           | 0.380        | 0.186        | 0.232         | 0.529         |              |
| Ci (μmol·mol⁻¹)                      |               |              |              |              |              |              |              |
| 100                                   | 223           | 208          | 251          | 218          | 231           | 239           | 174          |
| 69                                    | 228           | 207          | 273          | 222          | 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***         |
| R²                                    | 0.347         | --           | 0.696        | 0.692        | 0.557         | --            | 0.630        |

*PE 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, or 0.001 or nonsignificant, respectively, based on F values.

correlated to gs (R² = 0.11; results not shown). VPD accounted for ≈ 70% of the variation in gs (Fig. 1b). Transpiration rate (range = 5.0 to 7.8 mmol·m⁻²·s⁻¹) was seldom influenced by light regime. WUE (range = 0.9 to 2.5 mmol CO₂/mol H₂O) 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 average 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 × fiaseri (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 × fiaser 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 ± 8 µmol·m⁻²·s⁻¹; air temperature: SNLV = 28.4 ± 0.2C, SHLV = 28.9 ± 0.1C; leaf temperature: SNLV = 26.4 ± 0.3C, SHLV = 27.2 ± 0.3C; VPD: SNLV = 2.2 ± 1.1 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 was higher in 29%-sun leaves than in 100%-sun leaves. Leaf temperatures in 100% sun were 2 to 3C 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 (%) | 100 | 69 | 47 | 29 | Significance | $R^2$ |
|-----------------------|---------------------|-----|----|----|----|--------------|------|
| Increase in GI* (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.)*     |                     |     |    |    |    |              |      |
| 1987                  |                     | 82  | 120|123| 98|Q*          |0.40 |
| 1988                  |                     | 1005| 834|711|519|L***        |0.77 |
| Total leaf area (1000 cm²) |                 |     |    |    |    |              |      |
| 1987                  |                     | 1.27| 1.81|2.03|1.81|              |      |
| 1988                  |                     | 16.6| 14.4|13.5|10.2|L***        |0.63 |
| Area/leaf (cm²)       |                     |     |    |    |    |              |      |
| 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 |

*Increase in GI = (height + width)/2.

1Relative leaf total, total leaf area, area/leaf, dry weight/leaf, and specific leaf weight were determined from all leaves harvested.

2Relative leaf water content and leaf chlorophyll concentration were measured on RE and PE leaves.

 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 (MPa) | -0.88 | -1.00*** |
| Chlorophyll concn (µg·cm⁻²) | 37.2 | 56.4*** |
| Chl a : chl b | 2.82 | 2.52*** |

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

***, ** Significant at P = 0.01 or nonsignificant, respectively, by t test.

Phyll 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 gs appeared to be controlled by different environmental variables. The gs was inversely related to VPD (R² = 0.69; Fig. 2b), similar to that reported for other species (Mooney, 1983; Schulze and Hall, 1982; Turner et al., 1984). However, A was primarily influenced by PPF (R² = 0.60), not VPD (R² = 0.16). Thus, A and gs were not strongly coupled (R² = 0.13). In addition, the diurnal gs 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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