

# Net Photosynthesis and Transpiration of Sun- and Shade-grown *Ficus benjamina* Leaves<sup>1</sup>

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**Abstract.** Suitable conditions for determining net photosynthesis (Pn) of individual sun- and shade-grown leaves of weeping fig (*Ficus benjamina* L.) were 21°C dew point and an air flow rate between 1 and 3 liters/min. A diurnal trend in Pn occurred for sun leaves, with maximum rates between 0800 and 1200 HR; shade leaves did not decline in Pn until mid-afternoon. Leaves which originated from nodes 4 through 10 (from the shoot apex) did not differ in Pn, transpiration (Tr), specific leaf weight (SLW), or leaf water content. Shade-grown leaves had a photosynthetic advantage over sun-grown leaves at levels of photosynthetically active radiation (PAR) below 77  $\mu\text{E m}^{-2}\text{s}^{-1}$ , whereas at PAR levels above 100  $\mu\text{E m}^{-2}\text{s}^{-1}$  the reverse was true. Sun-grown leaves had higher Tr rates than shade grown leaves at all PAR levels used.

Transfer of weeping fig from production areas to low-light interior environments often results in severe leaf abscission. Light acclimatization improves the adaptation of plant species to low light (5, 6, 21) and in weeping fig has been found to affect leaf chlorophyll content (7, 10, 19), nonstructural carbohydrate content (17, 19), stomatal resistance (16), plant morphology (11, 15, 17), leaf anatomy (11), and the occurrence of leaf abscission after placement in a low-light environment (8, 9, 19).

Survival of plants under low light depends upon the efficiency with which leaves capture and utilize available light, and upon control of respiratory losses. Light compensation point (LCP) is a reflection of these factors and defines the limits of shade adaptability of a species. Collard et al. (7) determined whole plant LCPs of weeping fig plants grown under 4 radiation levels and found that the LCP of 80% shade-grown plants was only 36% that of full-sun-grown plants. Other researchers (15, 17) also reported lower whole plant LCPs for shade-grown weeping fig plants.

Although these data are useful in predicting adaptability to low light, they do not provide an indication of the photosynthetic potential of individual leaves. Since sun- and shade-grown weeping fig plants differ in morphology, variations in light penetration through the canopy due to differences in leaf size, leaf angle, lamina folding, branch angle, and internode spacing influence whole plant LCP.

The objectives of this research were to establish suitable laboratory conditions for measuring Pn on individual sun- and shade-grown weeping fig leaves, and determine the influence of production light regimes on Pn and Tr over a range of PAR levels.

## Materials and Methods

Cuttings were taken from a sun-grown greenhouse stock plant on Aug. 15, 1979, and rooted under mist. Six weeks later, rooted

cuttings were potted in 10.2-cm plastic pots filled with a peat-lite artificial medium (Pro-Mix, Premier Peat Moss Corp., New York, N.Y. 10036). Plants were greenhouse-grown in Blacksburg, Va. under natural photoperiod and prevailing irradiance (11) or 50% light exclusion provided by woven polypropylene shade fabric. By Feb. 21, 1980, there was little visual difference between treatments so the shade level was increased to 75% for the remainder of the experiment. Plants were repotted June 24, 1980, in 15.2-cm plastic pots and again on Dec. 3, 1980, in 7.6-liter plastic pots, using Pro-Mix each time. Plants were fertilized every 2 weeks October-March and weekly April-September with a water soluble 20N-8.7P-16.7K fertilizer (Peters 20-20-20, W. R. Grace & Co., Allentown, Pa. 18104) at 350 ppm N applied to field capacity.

*Laboratory conditions.* Pn was measured using the methods and apparatus described by Ferree and Barden (12) and Halfacre et al. (14), except that leaf chambers were redesigned to accommodate the short petioles of weeping fig leaves. Chamber lids, made by gluing a piece of plexiglas onto a wide-mouth canning jar lid, were bolted on a board with weather stripping as a sealant. A small notch filed in the canning jar lids allowed room for the petiole. Leaf chambers were 9 cm in diameter and 2 cm deep. To measure dark respiration (Rd), a similar set of chambers was painted black.

Four 500-W incandescent flood lamps provided a range of PAR levels controlled by varying the number of layers of polypropylene shade fabric with fine adjustments by regulating voltage. Except for the experiment with variable air flow rates, flow rates were maintained at 2 liters/min for Pn and 1 liter/min for Rd. Chamber air temperature was  $31 \pm 2^\circ\text{C}$  under saturation PAR levels, and  $24 \pm 1^\circ$  in darkness. Dew point of the air stream was measured with a dew point hygrometer (System 1100 AP, General Eastern Instruments Corp., Watertown, Mass. 02172). Dew point, regulated by bubbling the air stream through a flask of heated or cooled water, was  $18 \pm 2^\circ$  for all experiments except the one with variable dew points. Tr rates were calculated from the difference in dew point of the air before and after passing through the leaf chamber.

Plants were transported to the laboratory and watered thoroughly the evening prior to Pn determinations. Leaf areas were estimated by multiplying lamina length  $\times$  mid-lamina width by a factor of 0.65. Leaf area estimates by this method compared to areas obtained using an automatic area meter resulted in a *r* value of 0.99 (data not shown).

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**Dew point-air flow.** A  $3 \times 3 \times 2$  factorial experiment was designed to compare the effects of dew point (10.0, 15.5, and 21.0°C) and air flow rate (1, 2, and 3 liter/min) on Pn and Tr of sun- and shade-grown plants. For uniformity, the 4th fully expanded leaf from the shoot apex was sampled. Pn and Tr were measured on a single attached leaf on each plant at each dew point  $\times$  flow rate treatment in random order. Treatments were replicated 4 times. Two replications of sun- or shade-grown plants were sampled per day. Based on preliminary data, saturation PAR levels chosen for this experiment were 350 and 260  $\mu\text{E m}^{-2}\text{s}^{-1}$  for sun- and shade-grown leaves, respectively. PAR was measured with a LI-COR light meter (Model LI-185) using a quantum sensor (LI-COR, Inc., Lincoln, Neb. 68504). Data were collected May 27 and on June 3, 4, and 9, 1980.

**Diurnal trends.** A  $5 \times 2$  factorial experiment was designed to study diurnal trends in Pn and Tr of sun- and shade-grown leaves. Measurements were taken on the same leaves at five 2-hour intervals between 0800 and 1800 HR. Each treatment was replicated 6 times with 2 leaves per replication. The 6th fully expanded leaf from the shoot apex on 2 separate branches was sampled. Based on preliminary data, PAR levels chosen for these experiments were 350 and 260  $\mu\text{E m}^{-2}\text{s}^{-1}$  for sun and shade grown leaves, respectively.

Leaves were left in the chambers under saturating light for 30 min prior to each measurement. In this manner, 2 sun- and 2 shade-grown plants could be sampled within a 2-hour period, and the procedure repeated on the same leaves 4 more times throughout the day. Data were collected Jan. 31, and on Feb. 1, and 2, 1981.

**Leaf variation within a shoot.** A  $4 \times 2$  factorial experiment was designed to study the effect of leaf position on Pn (leaf area and dry weight bases), Tr, leaf water content, and SLW of sun- and shade-grown leaves. The 1st, 4th, 7th, and 10th fully expanded leaves were identified. Leaves at position 10 were estimated to be between 6 and 8 months old from full expansion. Pn and Tr were determined on each of the 4 leaves per branch in random order using a PAR level of 350  $\mu\text{E m}^{-2}\text{s}^{-1}$  for both sun- and shade-grown leaves. Treatments were replicated 10 times.

At the end of the day the sample leaves were removed, weighed, and dried. Leaf water content was calculated as percent water in fresh tissue. Data were collected Feb. 25, 26, and on March 2, 1981.

**Light response curves.** Pn and Tr were measured on sun- and shade-grown leaves at 8 PAR levels ranging from 30 to 545  $\mu\text{E m}^{-2}\text{s}^{-1}$ . The 6th fully expanded leaf from the shoot apex of 3 branches per plant was used for Pn, and from 1 branch for Tr. Each was replicated 9 times. Leaves were exposed to increasing PAR levels and left for 10 min at each PAR level before taking a reading. Rd was determined for each sample leaf the evening beforehand. Data were collected from Jan. 15 to Feb. 6, 1981.

## Results and Discussion

**Dew point-air flow.** Sun- and shade-grown leaves responded similarly to varying dew points, although sun leaf Pn and Tr rates were consistently higher (Table 1). There were no significant interactions between dew point and flow rate. Maximum Pn rates were obtained at a dew point of 21°C, while Tr generally decreased with increasing dew point. Flow rate had no effect on Pn, but Tr increased at the 2 higher flow rates.

Higher Pn rates with increasing dew points were probably a consequence of stomatal opening in response to improved leaf

Table 1. Main effects of dew point and flow rate on net photosynthesis (Pn) and transpiration (Tr) of full-sun- and 75% shade-grown weeping fig leaves.

Variable	Pn (mg CO <sub>2</sub> dm <sup>-2</sup> hr <sup>-1</sup> )			Tr (g H <sub>2</sub> O dm <sup>-2</sup> hr <sup>-1</sup> )		
	Sun	Shade	Means	Sun	Shade	Means
<i>Air dew point (°C)</i>						
10.0	8.3	7.8	8.1a'	1.6	1.1	1.3a
15.5	9.2	8.6	8.9b	1.5	1.0	1.3a
20.0	10.6	9.3	9.9c	1.2	0.7	0.9b
Means	9.3	8.6*		1.4	0.9*	
<i>Flow rate (liters/min)</i>						
1	9.5	8.7	9.1a	1.2	0.8	1.0a
2	9.2	8.5	8.9a	1.5	1.0	1.2b
3	9.3	8.5	8.9a	1.6	1.0	1.3b
Means	9.3	8.6*		1.4	0.9*	

'Mean separation within columns and variable by Duncan's multiple range test, 5% level.

\*Significant difference within rows within variable, 5% level.

water status, since at higher dew points, the vapor pressure gradient between the leaf and the air is reduced.

Since flow rate did not influence Pn, the leaf boundary layer resistance and CO<sub>2</sub> availability within the chamber were apparently not limiting Pn at the lowest flow rate because of inadequate air circulation and replacement. Pn of apple leaves reportedly increased with increasing flow rates between 1.0 and 2.5 liters/min (2). This increase in Pn was attributed to a concomitant decline in CO<sub>2</sub> depletion in the air stream. The low Pn rates of weeping fig leaves along with small leaf areas, compared to apple leaves, could account for the low acceptable flow rates to measure maximum Pn in weeping fig. Increased flow rate probably increased Tr by increasing the vapor pressure gradient between the leaf and the air. These data suggest that a dew point of 21.0°C is preferable to 10.0° or 15.5° for Pn determinations, while flow rates of 2 or 3 liters/min results in equally high rates as obtained at 1 liter/min.

**Diurnal trends.** Pn rates of shade-grown leaves were unaffected by time of day until approximately 1600 HR (Table 2); Pn rates of sun-grown leaves began to steadily decline around 1200 HR. By late afternoon, Pn rates of sun-grown leaves were only about a third of maximum. Tr rates of sun-grown leaves also began to decline somewhat earlier than for shade-grown leaves.

Pn data collected in late afternoon indicate that shade-grown leaves photosynthesize at higher rates than sun-grown leaves, while data collected at 1200 HR indicate the reverse to be true.

Table 2. Diurnal trends of net photosynthesis (Pn) and transpiration (Tr) of full-sun- and 75% shade-grown weeping fig leaves.

Time of day (HR)	Pn (mg CO <sub>2</sub> dm <sup>-2</sup> hr <sup>-1</sup> )		Tr (gH <sub>2</sub> O dm <sup>-2</sup> hr <sup>-1</sup> )	
	Sun	Shade	Sun	Shade
0800-1000	9.2a <sup>2</sup>	6.5a	1.0a	0.5a
1000-1200	9.7a	6.9a	1.1a	0.6a
1200-1400	8.0b	6.8a	1.0a	0.6a
1400-1600	5.3c	5.9a	0.6b	0.5a
1600-1800	2.9d	4.5b	0.4c	0.3b

<sup>2</sup>Mean separation in columns by Duncan's multiple range test, 5% level.

To obtain near maximum Pn rates and insure reproducible data, sun-grown leaves should be measured between 0800 and 1200 HR, while shade-grown leaves could be measured until approximately 1600 HR.

Since Pn and Tr follow the same general trends for both sun- and shade-grown leaves, and stomatal opening and closing can cycle diurnally (18), this diurnal trend in Pn could be a stomatal response. Previous problems in the laboratory with obtaining Pn rates on sun-grown leaves late in the afternoon support these findings. Prior light conditioning during the earlier part of the day appeared to have no effect on Pn, so that a buildup of assimilates in sun-grown leaves would not provide a satisfactory explanation for this decline in Pn.

**Leaf variation within a shoot.** Parameters measured for sun- and shade-grown plants were similar in leaves 4, 7, and 10 (Table 3). Thus, leaves 4–10 may be considered both physiologically and morphologically mature. Further, within a given environment, SLW and leaf water content may be useful indices of leaf maturity. SLW may also provide information on the light environment under which leaves developed (11). Pn rates of sun-grown leaves were higher than for shade-grown leaves on a leaf area basis (Table 3) while the reverse was true when calculated on a leaf dry weight basis. These differences are partially due to the greater leaf and lower SLW of shade-grown leaves as compared with sun-grown leaves.

Low Pn rates of leaf 1 may be related to incomplete development of the leaf mesophyll since newly expanded leaves have been observed to contain undifferentiated mesophyll cells; newly expanded leaves are not as thick as fully mature leaves and cuticle development may be incomplete (B. S. Fails, unpublished data). These factors would contribute to the low SLW and high leaf water content. New leaves may also be more subject to water stress in the leaf chamber, which would reduce both Tr and Pn if stomata were partially closed.

Data indicate that leaves 4–10 can be selected for Pn determinations. Photosynthesis reaches a maximum sometime after the lamina attains full size and does not decline appreciably for at least 6–8 months (Table 3).

**Light response curves.** Light response curves of photosynthesis for sun- and shade-grown weeping fig leaves are similar to those reported for a variety of other species (5, 6, 21). Shade-grown weeping fig leaves were light saturated at  $200 \mu\text{E m}^{-2}\text{s}^{-1}$ , while sun-grown leaves were saturated near  $350 \mu\text{E m}^{-2}\text{s}^{-1}$ . Shade-grown weeping fig leaves had a photosynthetic advantage over sun-grown leaves at PAR levels less than  $77 \mu\text{E m}^{-2}\text{s}^{-1}$  (Fig. 1), while sun-grown leaves assume a competitive advantage

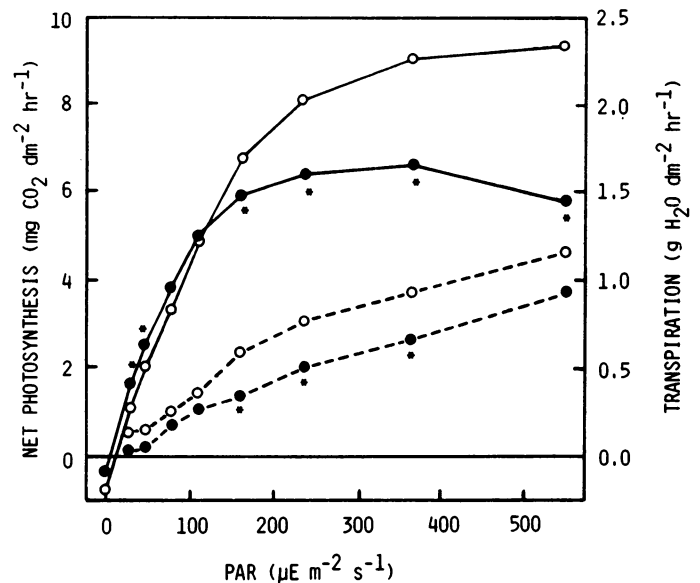


Fig. 1. The light response curves of net photosynthesis (solid lines) and transpiration (dotted lines) of full-sun-grown (open circles) and 75% shade-grown (closed circles) weeping fig. Mean separation between sun and shade leaves at each PAR level with an F test; \* = significant difference at 5% level.

at PAR levels higher than  $110 \mu\text{E m}^{-2}\text{s}^{-1}$ . Rd rates of shade-grown leaves ( $0.35 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ ), were half that of sun-grown leaves ( $0.75 \text{ mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ ), and LCPs for shade- and sun-grown leaves were 5 and  $11 \mu\text{E m}^{-2}\text{s}^{-1}$ , respectively.

Since these lines are nearly parallel in the low-light region of the response curve, the competitive advantage of shade-grown leaves can largely be explained by the control of respiratory losses. Survival of plants under extreme shade depends upon maximum interception and utilization of the available light, and reduction of substrate losses. Grime (13) found that Rd rates of shade plants were less than those of sun plants, the difference being most pronounced at high temperatures.

Leaf structure is one factor known to be modified by light (5, 20, 21) and may contribute to the photosynthetic advantage found for shade leaves in low light. Sun-grown weeping fig leaves are thick, have 2 layers of elongated palisade mesophyll cells, and chloroplasts align along the radial cell walls (11). In contrast, shade-grown leaves are thinner, have a single layer of short palisade cells, and chloroplasts are dispersed throughout

Table 3. Net photosynthesis (Pn), transpiration (Tr), specific leaf weight (SLW), and leaf water content of sun- and 75% shade-grown weeping fig leaves at different positions on a shoot.

Leaf no. from apex <sup>z</sup>	Parameter									
	Pn (area) ( $\text{mg CO}_2 \text{ dm}^{-2} \text{ hr}^{-1}$ )		Pn (dry weight) ( $\text{mg CO}_2 \text{ g}^{-1} \text{ hr}^{-1}$ )		Tr ( $\text{gH}_2\text{O dm}^{-2} \text{ hr}^{-1}$ )		SLW ( $\text{mg cm}^{-2}$ )		Leaf water (% fresh wt)	
	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade	Sun	Shade
1	3.1a <sup>y</sup>	4.0a	5.5a	8.9a	0.5a	0.6a	5.6a	4.3a	73.6a	75.3a
4	8.3b	6.4b	10.3b	11.6b	1.0b	0.7a	8.1b	4.8ab	66.2b	72.7a
7	8.1b	6.5b	8.7b	13.1b	1.0b	0.7a	9.4b	4.9b	64.2b	72.7a
10	9.2b	6.5b	10.0b	13.0b	0.9b	0.7a	9.4b	5.1b	64.8b	72.9a
Means	7.2	5.8*	8.6	11.6*	0.8	0.7*	8.1	4.8*	67.2	73.4*

<sup>z</sup>Leaf number refers to sequence of leaves from the shoot apex: leaf 1 = youngest fully expanded leaf.

<sup>y</sup>Mean separation within columns by Duncan's multiple range test, 5% level.

\*Significant difference within rows and within variables, 5% level.

the palisade cells and appear to be larger than in sun-grown leaves.

Chloroplasts of extreme shade leaves have been characterized by well-developed grana stacks (1) and the proportion of grana lamellae to stroma lamellae is higher than in sun leaves. Related to these structural differences, shade leaves also have a lower ratio of soluble protein to chlorophyll (1, 3) and a higher chlorophyll content per chloroplast (1). Researchers (1, 4) suggest that shade leaves invest more energy in the production of effective light-harvesting systems in relation to proteins. At saturating light, Pn (dry weight basis) was higher for shade than for sun leaves (Table 3). In low light, Pn (leaf area basis) was higher for shade than for sun leaves (Fig. 1). This data seems to support the hypothesis that shade leaves of weeping fig are more "cost efficient" under conditions of low light.

Tr rates increased sharply between 47 and 235  $\mu\text{E m}^{-2}\text{s}^{-1}$ , after which the increase was more linear (Fig. 1). Sun-grown leaves tended to transpire at higher rates than shade-grown leaves at all PAR levels. However, Tr rates were significantly different between sun- and shade-grown leaves at only 160, 235, and 365  $\mu\text{E m}^{-2}\text{s}^{-1}$ . Sun-grown weeping fig leaves have a higher stomatal density (11) and a lower leaf diffusive resistance (16), which may explain the higher Tr rates observed for sun-grown leaves. Increasing Tr rates from 30 to 235  $\mu\text{E m}^{-2}\text{s}^{-1}$  are likely due to increasing stomatal aperture, while further increases may be attributed to temperature, especially since shade-grown leaves are light saturated below 235  $\mu\text{E m}^{-2}\text{s}^{-1}$ . Leaf chamber air temperatures increased linearly with increasing PAR from 25°C at 160  $\mu\text{E m}^{-2}\text{s}^{-1}$  to 31° at 545  $\mu\text{E m}^{-2}\text{s}^{-1}$ . Increasing temperature increases the vapor pressure gradient between the leaf and the air, which could account for increased Tr rates despite partial stomatal closure, and could have some bearing on Pn measurements also.

Low LCP and Rd rates for shade-grown weeping fig plants explain the observation (10) that shade-produced plants survive better in low-light interior environments than plants produced in full sun. Comparisons among the previous reports (7, 15, 17) on whole plant LCP of sun- and shade-grown weeping fig plants indicate considerable variation, but LCP cannot be compared directly due to differing units of measure. However, their results generally concur with those reported herein which indicate considerable potential for photosynthetic adaptation of weeping fig leaves to varying light environments. Monitoring Pn of individual leaves during environmental changes could provide useful information on the acclimatization potential of mature leaves. This method would be especially informative since canopy morphology and production of new foliage are known to change with environment and would influence Pn determinations based on whole plants.

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