Light Acclimatization Potential of Ficus benjamina

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Abstract. Weeping fig (Ficus benjamina L.) plants grown under 3 light regimes (full sun, full sun followed by 8 weeks acclimatization under 75% shade, and 75% shade) were placed in a low-light simulated interior environment (SIE) for 12 weeks. Acclimatized and shade-grown leaves had higher net photosynthesis (Pn) rates, lower dark respiration (Rd) rates, and lower light compensation points (LCP) than sun-grown leaves after 12 weeks in the SIE. No treatments increased total plant dry weight during the 12 weeks of SIE. However, percent dry matter of sun plants was redistributed with additional leaves produced at the expense of root carbohydrate reserves. Leaf production exceeded abscission in all treatments. Anatomical observations prior to and following the SIE indicated chloroplast reorientation in all treatments. The development of large, heavily stained chloroplasts suggest ultrastructural changes may also occur as a result of low light.

Severe defoliation of weeping fig often occurs following transfer from production to interior environments, and is thought to at least partially result from the extreme reduction in light, since light acclimatization or production under shade reduces subsequent abscission (7, 8, 9, 10). Preconditioned plants generally have lower LCPs and Rd rates and adapt more successfully to low-light interior environments. Collard et al. (6) found that weeping fig plants grown under 80% shade had a LCP about one-third that of full-sun-grown plants. Johnson et al. (17) and Joiner et al. (18) reported that LCP of 47% shade-grown plants was less than that of full-sun-grown plants. Fonteno and McWilliams (13) reported that LCP and Rd of 4 sun-grown foliage species declined after transfer to a SIE for 4 to 15 weeks. These reports were based on whole plant determinations; variation in light measurements and rates of Pn due to differing canopy morphology were not examined. Pn and Rd of individual leaves could minimize inconsistencies.

There is little information regarding the potential of mature weeping fig leaves to photosynthetically acclimatize to extreme light reductions or the influence of production light environment on acclimatization potential. Conover and Poole (8) suggested that little shade conversion of sun-grown foliage occurred during acclimatization, rather the advantage of acclimatization being the production of new shade-grown foliage and conversion of immature foliage. Light during development affects both leaf anatomy and physiology in weeping fig (11, 12) and in other species (4, 5, 19). The extent to which light acclimatization can occur without concomitant changes in leaf anatomy is unknown.

The objectives of this study were to determine the effect of light preconditioning on the acclimatization potential of weeping fig by examining Pn, Rd, LCP, leaf anatomy, and various growth parameters.

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 peatlite 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 7.6liter plastic pots. 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.

Plants were placed in a SIE after production in full sun (S-SIE), 75% shade (Sh-SIE), or full sun followed by 8 weeks acclimatization under 75% shade (A-SIE). Two additional groups, full sun (S) and 75% shade grown (Sh), remained under respective production light regimes and served as controls. Data were collected after 0, 6, and 12 weeks in the SIE, excepting leaf abscission data which were recorded weekly. There were 10 plants per treatment.

Terminal leaves were labeled November 5, at which time plants in treatment A-SIE were placed under 75% shade for 8 weeks acclimatization.

The SIE, approximately 7.5 m^2 , was enclosed in black plastic. Light was provided by 6 Cool-White fluorescent lamps approximately 2 m above floor level. PAR measured with a LI-COR light meter and a 190S quantum sensor (LI-COR, Inc., Lincoln, Neb. 68504) was 20 $\mu \text{E} \text{ m}^{-2} \text{ s}^{-1}$ at plant height and the photoperiod was 16 hours. The SIE was vented above 24°C during the day and thermostatically set at 18° nights. Plants in the SIE were not fertilized.

Week 0. On December 29, one mature leaf (the 5th fully expanded leaf from a shoot apex) from each plant was collected. Small, rectangular sections were cut at mid-lamina, preserved in formalin-acetic acid-alcohol, dehydrated in an ethanol-xylene series using an automatic tissue processor, and embedded in paraffin; 10 μ m sections were stained with safranin and fast green.

Rd, Pn, and LCP were determined on 2 leaves per plant (each the 5th fully expanded leaf from a shoot apex) as described

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previously (12). Rd was determined after plants had been in a dark laboratory for 1 hour. An air flow rate of 1 liter/min was used; chamber air temperature was $24 \pm 1^{\circ}$ C. Pn was measured on the same leaves under a saturating PAR of 365 μ E m⁻²s⁻¹ and a flow rate of 3 liters/min. Identical PAR levels were used to determine Pn for all light regimes; leaves were exposed to saturating light 15–30 min before measuring Pn. LCP was determined by gradually reducing PAR to a point where no net change in CO₂ concentration occurred and remained constant for at least 5 min.

A random sample of 20 leaves per treatment was collected to estimate leaf area using the formula: lamina length \times width \times 0.65 (12). Total leaf area was calculated by multiplying average leaf area by leaf number. Specific leaf weight (SLW) samples were collected and fresh and dry weights of leaves stems, and roots recorded. Terminal leaves were labeled on remaining plants in all treatments.

Data were analyzed by analysis of variance. Inasmuch as there were no differences in prior handling of treatments S and S-SIE or Sh and Sh-SIE at week 0, data were collected from only S-SIE, Sh-SIE and A-SIE plants at week 0.

Week 6. Pn, Rd, and LCP were again determined in treatments S-SIE, A-SIE, and Sh-SIE on the same leaves measured at week 0. Pn, Rd, and LCP were also measured in treatments S and Sh



Fig. 1. Weeping fig plants grown under 3 light regimes, left to right, A) full-sun control (S), full sun followed by 12 weeks in a simulated interior environment (S-SIE), full sun plus 8 weeks acclimatization under 75% shade followed by 12 weeks in a SIE (A-SIE), B) 75% shade control (Sh), 75% shade followed by 12 weeks in a SIE (Sh-SIE).

using the 5th fully expanded leaf from a shoot apex as established at week 0.

Week 12. Pn was measured at 8 increasing PAR levels ranging from 30 to 545 μ E m⁻²s⁻¹ on 1 of the 2 leaves measured previously on each plant. Rd was measured as previously described. LCP was interpolated from the resulting light response curves. Pn rates at 365 μ E m⁻²s⁻¹ were compared with Pn data from weeks 0 and 6.

The 5th fully expanded leaf from a shoot apex at week 0 was collected for anatomical study and processed as previously described.

Plants in all treatments were harvested as described at week 0. Leaves were categorized as maturing prior to week 0 (old) and after week 0 (new). SLW samples were collected and leaf area and fresh and dry weights were determined for new and old leaves, stems, and roots.

Results and Discussion

Growth. Plants showed no visual signs of deterioration during 12 weeks in the SIE (Fig. 1). Despite the extreme light reduction, all treatments exhibited a net gain in leaf number. New leaf production averaged 59, 45, and 31 for S-SIE, A-SIE and Sh-SIE, respectively (Table 1); leaf abscission averaged 15, 16, and 5 leaves/plant, respectively.

These results are inconsistent with those of Conover and Poole (7, 9) who reported considerable leaf abscission on plants produced in full sun or full sun grown/acclimatized after transfer to an interior environment. However these studies are not directly comparable, inasmuch as the magnitude of the original light level and the light reduction differed between the two studies.

Although fewer leaves were produced on Sh-SIE than on S-SIE plants, they were larger (Table 1). As a result, total leaf area did not differ among treatments in the SIE. SLW of new foliage in S-SIE plants was greater than Sh-SIE, but less than S plants. SLW appears to be influenced not only by the light environment under which the leaf develops, but to some extent by previous light history of the plant as well. No changes in SLW occurred in old leaves in any treaatment after 12 weeks in the SIE (Table 2).

No SIE treatments increased in dry weight (Table 2). Gains in leaf tissue dry weight of S-SIE plants appear to have occurred at the expense of root reserves, especially since these plants

Table 1. Leaf growth of weeping fig produced under 3 light regimes and placed in a simulated interior environment (SIE) for 12 weeks compared to sun- and shade-grown controls. Data refer to new leaves produced during the 12 week period.

	Light regime ^z						
Variable	S (control)	Sh (control)	S-SIE	A-SIE	Sh-SIE		
Leaves produced	254a ^y	49bc	59b	45bc	31c		
Total leaf area (cm ²)	3764a	902ь	682bc	456c	446c		
Average leaf area (cm ²)	14.8b	18.3a	11.5c	10.1c	14.2b		
Specific leaf weight (mg	5.0	2.01	4.21	4.01	2.6		
cm ²)	5.9a	3.9bc	4.3b	4.0bc	3.60		

^zS-full sun grown, Sh-75% shade grown, A-full sun grown followed by 8 weeks acclimatization under 75% shade.

^yMean separation in rows by Duncan's multiple range test, 5% level.

Table 2. Growth parameters of weeping fig produced under 3 light regimes and placed in a simulated interior environment (SIE) for 12 weeks compared to sun- and shade-grown controls.

		Harvest date (week)	Light regime ²					
Variable			S (control)	Sh (control)	S-SIE	A-SIE	Sh-SIE	
SLW of old leaves (mg cm $^{-2}$)		0			7.8a	7.2b	4.5c	
		12	7.1a ^y	4.6b	7.5a	7.1a	4.4b	
Whole plant dry weight (g)		0			151a	128b	59c	
		12	255a	85c	140b	126b	68c	
Dry matter distribution:								
(% of total dry weight)	Leaves	0			30.8b	33.4b	38.9a	
		12	30.7c	35.0ab	33.8b*	33.6b	37.2a	
	Stems	0			33.0b	34.8b	48.5a	
		12	40.3c	52.1a	34.2d	35.8d	48.0b	
	Roots	0			35.8a	31.8b	12.7c	
		12	29.0a	12.9b	31.0a*	30.6a	14.7b*	

^zS-full sun-grown, Sh-75% shade-grown, A-full sun-grown followed by 8 weeks acclimatization under 75% shade.

^yMean separation in rows by Duncan's multiple range test, 5% level.

*Significant difference within columns and variable, 5% level.

produced the greatest number of leaves in the SIE (Table 1). Final dry weight distribution of S-SIE plants was very similar to that of A-SIE plants. Milks et al. (20) reported that sun-grown plants had 29% higher root carbohydrate content than plants grown in 63% shade. But, after 3 months in a SIE, there was a 27% reduction in root carbohydrates in sun-grown plants resulting in similar carbohydrates levels for both sun-grown and shade-grown plants.

Net photosynthesis. Pn rates of A-SIE and Sh-SIE leaves were similar (Table 3) at week 0, although both were lower than S-SIE leaves. Pn decreased in all SIE treatments with time. By week 6, any effect of light preconditioning on light-saturated Pn rates was apparently lost, inasmuch as the 3 SIE treatments were similar. Pn at saturation has been reported to decline in species transferred from high- to low-light environments (3, 4, 19);

Table 3. Net photosynthesis (Pn), dark respiration (Rd), and light compensation point (LCP) of weeping fig leaves produced under 3 light regimes measured 0, 6, and 12 weeks after placement in a simulated interior environment (SIE), compared to sun and shade grown controls.

Variable ^y	Observation date (wk)	Light regime ²					
		S (control)	Sh (control)	S- SIE	A- SIE	Sh- SIE	
Pn (mg CO ₂							
dm ⁻² hr ¹)	0		—	9.7a	8.0b	6.9b	
	6	9.0a ^y	6.8b	5.9bc	6.4bc	5.5c	
	12	8.2a	6.3b	3.4c	3.9c	3.5c	
Rd (mg CO ₂							
$dm^{-2} hr^{-1}$)	0	_		.75a	.33b	.31b	
	6	.79a	.35ь	.35b	.35b	.25c	
	12	.70a	.26b	.26b	.23b	.20b	
LCP							
$(\mu E m^{-2}s^{-1})$	0			12a	7b	4c	
	6	11a	4cd	6b	6bc	3d	
	12	14a	6c	10b	7c	6c	

²S-full sun grown, Sh-75% shade grown, A-full sun grown followed by 8 weeks acclimatization under 75% shade.

^yMean separation in rows by Duncan's multiple range test, 5% level.



Fig. 2. Light response curves of net photosynthesis (Pn) of weeping fig grown under full sun (S-SIE), 75% shade (Sh-SIE), and full sun plus 8 weeks acclimatization under 75% shade (A-SIE), and placed in a simulated interior environment (SIE) for 12 weeks compared to full sun (S) and 75% shade (Sh) controls. Mean separation at each PAR level by Duncan's multiple range test, 5% level.

lower maximum Pn rates are typical of shade-grown leaves (4, 5, 12).

Rd of A-SIE and Sh-SIE leaves at week 0 was lower than that of sun leaves (S-SIE). Rd decreased markedly by week 6 in S-SIE and by week 12, there was no difference in Rd among the Sh and SIE treatments, indicating that adaptation was occurring. Lower respiratory losses in shade-grown plants have been reported for weeping fig (12) and other species (3, 14). This adaptation reduces substrate losses and contributes to the low LCP typical of shade-adapted leaves.

LCP of acclimatized leaves (A-SIE) at week 0 was lower than that of sun-grown leaves (S-SIE), but higher than that of shade-



Fig. 3. Cross sections of weeping fig leaves produced in 3 light environments followed by 12 weeks in a simulated interior environment (SIE) under 20 μ E m⁻²s⁻¹. A) full sun prior to and B) after SIE; C) full sun followed by 8 weeks acclimatization under 75% shade prior to and D) after SIE; E) 75% shade prior to and F) after SIE. Bar represents 50 μ m.

grown leaves (Sh-SIE). By week 12, leaves of S-SIE plants had a LCP lower than full sun-grown (S) leaves, but higher than A-SIE and Sh-SIE leaves.

At week 12, Sh-SIE and A-SIE did not differ in the light response curves of photosynthesis. The lower portion of the curves is shown in Fig. 2. Leaves of S-SIE plants had a lower photosynthetic capacity than Sh-SIE and A-SIE plants at 30 and 47 μ E m⁻²s⁻¹. Low S-SIE rates in this region of the response curve cannot be attributed to high respiratory losses, since Rd did not vary among the SIE treatments. Leaves in both S-SIE and A-SIE developed under identical conditions in full sun.

Those leaves receiving 8 weeks acclimatization prior to placement in the SIE were better adapted photosynthetically than nonacclimatized leaves after 12 weeks in a SIE. Furthermore, they were equally as adaptable as shade-grown (Sh-SIE) leaves.

Leaf anatomy. Sun leaves at week 0 were thick, had multiple layers of palisade cells (Fig. 3A) and were characterized by other sun-adaptation features described previously (11). Chloroplasts within the palisade cells were aligned along the radial walls and did not stain heavily. After 12 weeks in the SIE, chloroplasts appeared larger, stained more heavily, and were dispersed throughout the palisade cells (Fig. 3B). Chloroplasts of acclimatized leaves (A-SIE) at week 0 (Fig. 3C) were similar to those of S-SIE leaves at week 12, although the degree of chloroplast modification was intermediate between that observed for S-SIE leaves at weeks 0 and 12. Acclimatized leaves at week 12 (Fig. 3D) were similar to S-SIE leaves at week 12.

Leaves of shade-grown plants at week 0 were thin, had a single layer of palisade cells (Fig. 3E), and were characteristic of shade-adapted weeping fig leaves (11). No apparent changes within the mesophyll occurred in shade-grown leaves (Sh-SIE) after 12 weeks in the SIE (Fig. 3F). Leaves which developed under SIE light displayed typical shade-leaf anatomy regardless of previous light conditioning.

Reorientation of chloroplasts to low light has been reported in other species (16) and is believed to maximize interception of available light by exposing the greatest area of chloroplasts. Structural modifications within the chloroplasts themselves may occur as a result of reduced light (2). Grana stacks have been reported more highly developed in low light (2, 5, 15, 21); a higher density of light harvesting assemblies contributes to more efficient collection of light quanta for photosynthesis. Anderson et al. (1) found shade-leaf chloroplasts to contain more chlorophyll, which may also occur during acclimatization of weeping fig leaves as suggested by heavier staining and larger chloroplast size.

Leaves of S-SIE closely resembled A-SIE leaves at week 12. Thus, differences in photosynthetic potential of acclimatized and nonacclimatized plants cannot be attributed solely to anatomy. Furthermore, basic leaf structure does not appear to limit photosynthetic adaptation of sun-grown leaves, since full sun-grown/ acclimatized leaves (A-SIE) were of similar photosynthetic potential to shade-grown leaves (Sh-SIE) after 12 weeks in the SIE despite differing mesophyll structure. Chloroplast reorientation and ultrastructural changes may, however, contribute to shadeadaptation of weeping fig leaves.

Due to mutual shading within the canopy, light available to most leaves was considerably less than the 20 μ E m⁻²s⁻¹ at plant height. LCP data indicate that at week 12 at least 6–10 μ E m⁻²s⁻¹ was required to maintain an individual leaf; these estimates do not account for stem and root respiratory demands or plant Rd at night. It is unlikely that the production of new shade-adapted foliage during the SIE phase could have met whole plant carbohydrate demands, as so few leaves developed in comparison to total plant size.

Thus it appears that a combination of reduced LCP and Rd, utilization of stored reserves, chloroplast reorientation and ultrastructural modifications, and the production of new shade foliage most likely contribute to the successful acclimatization of weeping fig plants to low-light interior environments.

Literature Cited

 Anderson, J. M., D. J. Goodchild, and N. K. Boardman. 1973. Composition of the photosystems and chloroplast structure in extreme shade plants. Biochim. Biophys. Acta 325:573-585.

- 2. Ballentine, J. E. M. and B. J. Forde. 1970. The effect of light intensity and temperature on plant growth and chloroplast ultrastructure in soybean. Amer. J. Bot. 57:1150–1159.
- 3. Barden, J. A. 1974. Net photosynthesis, dark respiration, specific leaf weight, and growth of young apple trees as influenced by light regime. J. Amer. Soc. Hort. Sci. 99:547-551.
- 4. Bjorkman, O. and P. Holmgren. 1963. Adaptability of the photosynthetic apparatus to light intensity in ecotypes from exposed to shaded habitats. Physiol. Plant. 16:889-914.
- Chabot, B. F. and J. F. Chabot. 1977. Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. Oecologia 26:363–377.
- Collard, R. C., J. N. Joiner, C. A. Conover, and D. B. Mc-Connell. 1977. Influence of shade and fertilizer on light compensation point of *Ficus benjamina* L. HortScience 102:447–449.
- 7. Conover, C. A. and R. T. Poole. 1973. Ficus benjamina leaf drop. Flor. Rev. 151(3925):29, 67, 68.
- 8. Conover, C. A. and R. T. Poole. 1975. Acclimatization of tropical trees for interior use. HortScience 10:600–601.
- 9. Conover, C. A. and R. T. Poole. 1977. Effects of cultural practices on acclimatization of *Ficus benjamina* L. J. Amer. Soc. Hort. Sci. 102:529-531.
- Conover, C. A., R. T. Poole, and R. W. Henley. 1975. Growing acclimatized foliage plants. Fla. Fol. Grow. 12(9):1–4.
- Fails, B. S., A. J. Lewis, and J. A. Barden. 1982. Anatomy and morphology of sun- and shade-grown *Ficus benjamina*. J. Amer. Soc. Hort. Sci. 107:754–757.
- Fails, B. S., A. J. Lewis, and J. A. Barden. 1982. Net photosynthesis and transpiration of sun- and shade-grown *Ficus benjamina* leaves. J. Amer. Soc. Hort. Sci. 107:758-761.
- Fonteno, W. C. and E. L. McWilliams. 1978. Light compensation points and acclimatization of four tropical foliage plants. J. Amer. Soc. Hort. Sci. 103:52-56.
- 14. Grime, J. P. 1965. Shade tolerance in flowering plants. Nature 208:161-163.
- 15. Hariri, M.and J. Brangeon. 1977. Light-induced adaptive responses under greenhouse and controlled conditions in the fern *Pteris cretica* var. *ouvardii*. I. Structural and instrastructural features. Physiol. Plant. 41:280–288.
- Haupt, W. 1973. Role of light in chloroplast movement. Bio-Science 23:289–296.
- Johnson, C. R., J. K. Krantz, J. N. Joiner, and C. A. Conover. 1979. Light compensation point and leaf distribution of *Ficus benjamina* as affected by light intensity and nitrogen-potassium nutrition. J. Amer. Soc. Hort. Sci. 104:335–338.
- Joiner, J. N., C. R. Johnson, and J. K. Krantz. 1980. Effect of light and nitrogen and potassium levels on growth and light compensation point of *Ficus benjamina* L. J. Amer. Soc. Hort. Sci. 105:170-173.
- Louwerse, W. and W. V. D. Zweerde. 1977. Photosynthesis, transpiration, and leaf morphology of *Phaseolus vulgaris* and *Zea* mays grown at different irradiances in artificial and sunlight. Photosynthetica 11:11-21.
- Milks, R. R., J. N. Joiner, L. A. Garard, C. A. Conover, and B. Tjia. 1979. Influence of acclimatization on carbohydrate production and translocation of *Ficus benjamina* L. J. Amer. Soc. Hort. Sci. 104:410-413.
- 21. Wilkinson, J. F. and J. B. Beard. 1975. Anatomical responses of 'Merion' Kentucky bluegrass and 'Pennlawn' red fescue at reduced light intensities. Crop. Sci. 15:189–194.