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J. Amer. Soc. Hort. Sci. 107(5):754–757. 1982.

Anatomy and Morphology of Sun- and Shade-grown *Ficus benjamina*¹

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Additional index words. acclimatization, weeping fig

Abstract. Weeping fig (*Ficus benjamina* L.) plants were greenhouse-grown under full sun or 75% light exclusion. Shade-grown leaves were larger, thinner, flatter, and darker green than sun-grown leaves. Sun- and shade-grown plants had the same total leaf area and were the same height. Shade-grown leaves had a single, poorly developed palisade layer with large chloroplasts dispersed throughout the palisade cells. Sun-grown leaves had one or two layers of well developed palisade cells with the chloroplasts aligned primarily along the radial walls. Stomatal density was greater in sun-grown leaves, but shade-grown leaves had more stomata per leaf.

Weeping fig, widely grown as a foliage plant and extensively used for commercial interior plantscaping, often drops many leaves when moved from production to interior locations. The extreme reduction in light levels has been considered a major cause of subsequent leaf abscission and has led to studies regarding light acclimatization of *Ficus* (5, 10, 11).

Adaptation to low light varies among species and is influenced genetically as well as by previous light history (3, 12). Shade adaptation ultimately depends upon the efficiency with which available light is intercepted and utilized for photosynthesis. Plant morphology and leaf anatomy influence adaptation by regulating light penetration through the canopy and light interception by the leaf. The modification of leaf anatomy and morphology as a response to light has been reported for other species (3, 6), but not for weeping fig.

The objectives of this study were to characterize the growth, morphology, and leaf anatomy of weeping fig plants grown under high- and low-light levels.

¹Received for publication Oct. 13, 1981.

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.

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Materials and Methods

Cuttings were taken from a sun-grown 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 (Table 1) or under 50% light exclusion provided by woven polypropylene fabric. There were 10 plants per treatment arranged in a randomized block design. On Feb. 21, 1980, the shade level was increased to 75% light exclusion because there was little visual difference between treatments. At that time, terminal leaves of all plants were marked so that subsequent growth could be identified. All plants were fertilized every 2 weeks 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 until April, then weekly until June 20, 1980. The greenhouse was vented above 24°C during the day and thermostatically set at 18° nights.

Morphological study. Leaves were removed and categorized as those which developed before February 21 (old), or after February 21 (new). Specific leaf weight (SLW) samples were collected and leaf areas determined using an automatic area meter. Lamina angle was determined from a random sample of 10 new leaves per plant, by placing a 2-mm-wide cross section of the widest part of the lamina against a protractor. Trunk

Table 1. Mean daily radiant energy flux August, 1979 to December, 1980, Blacksburg, Va.

Month	Radiant energy (cal/cm ²)	
	1979	1980
January		173
February		356
March		354
April		615
May		607
June		679
July		668
August	637	645
September	409	492
October	361	331
November	239	251
December	271	191

diameter 1 cm above the soil line was measured. Shoot growth after February 21 was measured and divided by the number of nodes to determine average internodal length. Plants were watered the night before harvest and leaves removed the following morning. Fresh and dry weights of plant leaf and aboveground stem tissue were recorded. Tissue water was calculated as percent water in fresh tissue.

Anatomical study. Three mature leaves per plant were selected at harvest. Each leaf used was the third fully expanded leaf from the shoot apex and had developed after February 21. Stomatal impressions were obtained from the abaxial leaf surface in an area approximately 1 × 4 cm using the method described by Wolf et al. (15). Stomata were counted at 300× along the laminar impression in 10 randomly chosen microscope fields per leaf. The estimated number of stomata per leaf was calculated by multiplying stomatal density by average leaf area. From these same leaves, small rectangles 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. Sections cut at 10 μm were stained with safranin and fast green. Leaf thickness at the laminar midpoint was measured with an eyepiece micrometer.

Results and Discussion

Morphological study. No leaf drop occurred after plants were moved from 50% to 75% shade. Plants grown in full sun had 49% more total leaves than plants grown in 75% shade (Table 2), but shade-grown leaves were 37% larger. As a result, the total leaf area did not differ. Shade-grown plants had longer

Table 2. Morphological characteristics of 9-month-old weeping fig plants greenhouse-grown under full sun or 75% shade.

Variable	Light regime		
	Sun	Shade	Significance
Leaves per plant	171	115	**
Total leaf area (cm ²)	2189	2012	NS
Average leaf area (cm ²)	12.8	17.5	**
Average internode length (cm)	2.6	3.8	**
Trunk diameter at base (mm)	11.5	8.3	**
Plant height (cm)	69	78	NS
Lamina angle (degrees)	111	153	**

NS. **Nonsignificant (NS) or significant difference between light regimes at 1% (**) level by *t*-test.

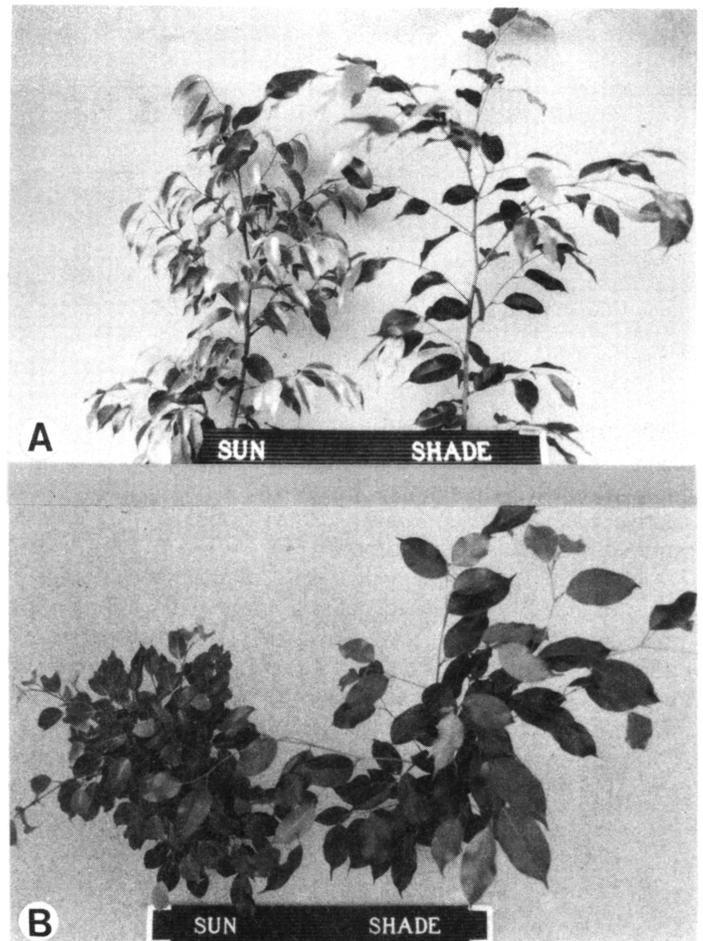


Fig. 1. Morphology of weeping fig plants grown under full sun or 75% shade. A) Side view of plant density, branch and leaf orientation. B) Overhead view of leaf size and arrangement.

internodes and smaller trunks; plant height did not differ. Shade-grown leaves had a 38% greater lamina angle than sun-grown leaves, and were held on the branch in a more horizontal plane (Fig. 1). There were fewer branches on shade-grown plants and branches were more horizontally oriented than on sun-grown plants, contributing to increased canopy diameter and a weeping growth habit. Sun-grown plants were compact and had upright branches with light-green foliage oriented more vertically.

Similar morphological observations for sun- and shade-grown weeping fig have been reported (5, 11), and suggest that shade-grown plants are better adapted to utilize light due to a more open canopy morphology. Although sun- and shade-grown plants had the same total leaf area, less direct radiation may actually penetrate the canopy of shade-grown plants due to the horizontal leaf and branch orientation and flatter lamina. Little new growth developed at the base of shade-grown plants. The suggested adaptive value of horizontal leaf orientation of shade-grown dicots lies in the interception of light at least expense, whereas the vertical orientation of sun-grown leaves enhances the photosynthetic capacity of individual leaves within the canopy by reducing mutual shading (13). Long internodes and few branches of shade-grown weeping fig plants contribute to a more open growth habit, which would likely afford greater penetrability of diffuse radiation.

SLW was 47% higher in sun-grown leaves (Table 3). Higher SLW has been reported for a number of plants grown in full sun (4, 6, 14). Total leaf and stem dry weights were 61 and 78%

Table 3. Growth characteristics of 9-month-old weeping fig plants greenhouse-grown under full sun or 75% shade.

Variable	Light regime		
	Sun	Shade	Significance
Specific leaf weight (mg cm^{-2})	8.4	5.7	**
Total leaf dry weight (g)	18.3	11.4	**
Total stem dry weight (g)	13.5	7.6	**
Leaf water content (%)	68	72	**
Stem water content (%)	67	73	**

**Significant difference between light regimes, 1% level by *t*-test.

greater, respectively, for sun-grown plants than for shade-grown plants. Shade-grown leaves had higher leaf and stem water contents; within a light regime, leaves and stems had the same relative water contents. Higher leaf water contents have been reported in shade rainforest species (3).

Anatomical study. Anatomical observations showed 1 or 2 layers of narrow, elongated palisade mesophyll cells in sun-grown leaves; in shade-grown leaves only 1 layer of short palisade cells developed (Fig. 2). Sun-grown leaves were 33% thicker than shade-grown leaves (Table 4), due to the greater thickness of both the palisade and the spongy parenchyma layers. A higher proportion of palisade to spongy mesophyll tissue developed in full sun than in shade. Since the palisade parenchyma

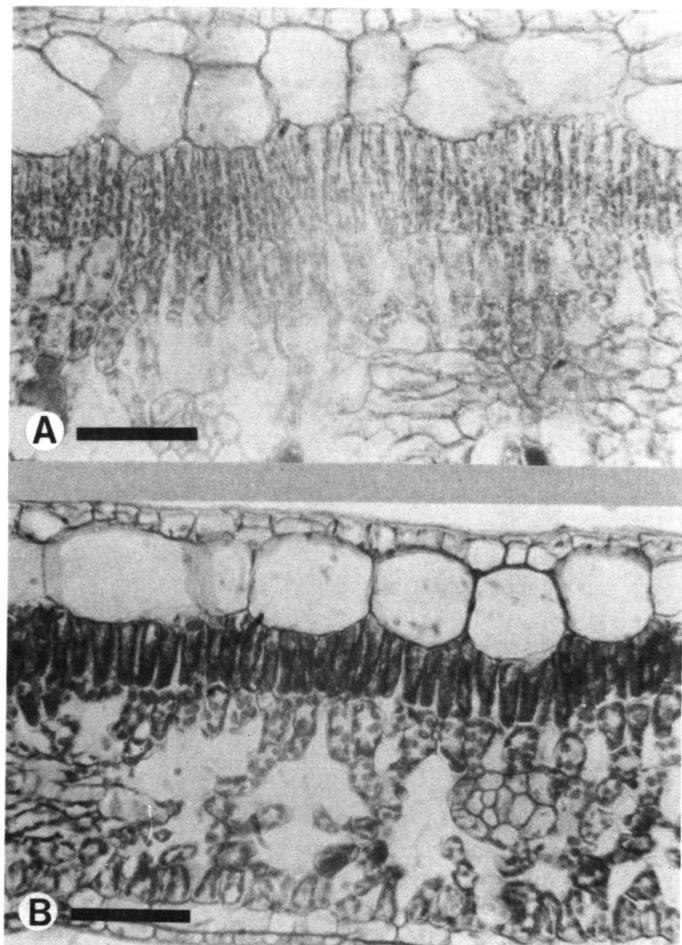


Fig. 2. Cross sections of weeping fig leaves illustrating differences in leaf mesophyll structure. A) Full sun grown. B) 75% shade grown. Bar represents 50 μm .

Table 4. Anatomical characteristics of 9-month-old weeping fig plants greenhouse-grown under full sun or 75% shade.

Variable	Light regime		
	Sun	Shade	Significance
Thickness (μm)			
Total leaf	247	186	**
Hypodermis	35	32	NS
Palisade	76	45	**
Spongy mesophyll	101	79	**
Stomata per mm^2	262	214	**
Stomata per leaf (1000)	298	391	**

NS. **Nonsignificant (NS) or significant difference between light regimes at 1% (** level by *t*-test.

is the most highly specialized type of photosynthetic tissue and contains most of the chloroplasts (7), the potential exists for increased photosynthesis in sun-grown leaves.

From visual observations, shade-grown leaves appeared to have more widely spaced veins and a greater proportion of intercellular space in the spongy parenchyma. These differences may be due in large part to greater cell elongation in shade, as mesophyll cells in shade-leaf cross sections were notably spaced further apart (Fig. 2). Leaves grown in full sun often had multiple layers of hypodermal cells (Fig. 2), which are believed to func-

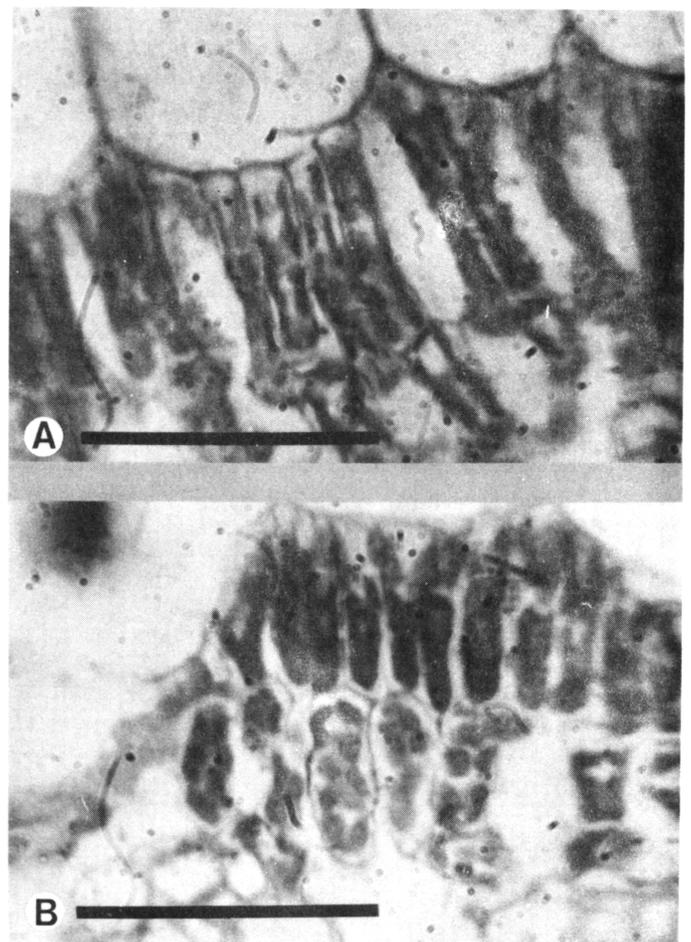


Fig. 3. Cross sections of weeping fig leaves illustrating orientation of chloroplasts in palisade cells. A) Full sun grown. B) 75% shade grown. Bar represents 50 μm .

tion in water storage (7), although thickness of the hypodermal layers did not differ from shade-grown leaves (Table 4).

Chloroplasts in shade-grown leaves stained more heavily than in sun-grown leaves, appeared to be larger, and were dispersed throughout the palisade cells (Fig. 3). The same levels of chlorophyll on a leaf area basis for full sun and 47% shade-grown weeping fig leaves have been reported (11), but chlorophyll on a leaf dry weight basis is generally higher in shade leaves of other species (2, 3, 6). Shade plants have a higher chlorophyll content per chloroplast (1), and grana stacks are more highly developed in low light (1, 2, 8). Thus structural differences within the chloroplasts themselves may contribute to a higher density of light-harvesting assemblies and more efficient collection of light quanta. Chloroplast orientation in low light tends to maximize exposure of total chloroplast area, further enhancing light interception (9). Ultrastructural and biochemical modifications of the chloroplasts may also contribute to shade adaptation of weeping fig.

Stomatal density was greater in sun-grown leaves, although shade-grown leaves had more total stomata (Table 4). There was no apparent difference in the size of individual stomata between treatments. Lower stomatal densities have been reported for other species grown in low light (6, 8) and for weeping fig grown under 47% shade (10). Differences in stomatal density between sun- and shade-grown leaves cannot be explained entirely by different rates of cell expansion, since the number of stomata per leaf was not the same; light environment may affect epidermal cell division or differentiation.

Sun- and shade-grown weeping fig plants display morphological and anatomical features typical of sun and shade adaptation. Based on the differential response to the two light environments, weeping fig appears to have potential to adapt to a wide range of light environments. Leaf mesophyll structure and chloroplast orientation and ultrastructure may be important in the adaptation of weeping fig plants to low light interior environments.

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