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Light Acclimation in Citrus Leaves. I. Changes in Physical Characteristics, Chlorophyll, and Nitrogen Content

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Abstract. **'Duncan' grapefruit (*C. paradisi* Macf.) and 'Pineapple' sweet orange (*Citrus sinensis* L.) seedlings were grown in full sunlight, 50% and 90% shade; maximum photosynthetic photon flux densities (PPFD) of 2300, 1100 and 200 μmol $s^{-1}m^{-2}$, respectively. In fully expanded matured (hardened) leaves, leaf thickness, specific leaf weight (SLW), tissue density, and nitrogen content were highest in full sun leaves and lowest in 90% shade leaves. Leaf chlorophyll content was highest in 90% shade leaves. Half of the seedlings which were grown in full sunlight were transferred into 50% shade to simulate normal canopy development; half of the seedlings from 50% and 90% shade were moved into full sunlight to simulate changes that occur after hedging. Specific leaf weight and tissue density changed in the same direction as PPFD. Leaf nitrogen content decreased temporarily when leaves were exposed to new PPFD conditions regardless of the PPFD levels. Total leaf chlorophyll content initially decreased when seedlings were transferred into full sunlight but began to increase after 4–6 weeks. Chlorophyll content increased in seedlings transferred from full sun to 50% shade. Percentage of air space within leaf tissues did not change during acclimation to new PPFD levels. Changes in leaf anatomy, physical characteristics, and chemical components are mechanisms that enable citrus leaves to acclimate to a wide range of changing light environments, even after leaves are fully mature.**

There is a world trend towards the use of high-density planting of virtually all tree fruit crops (6) including citrus (23, 34, 35). High density plantings tend to improve yield on a per hectare basis while trees are young (18, 23), but production and fruit quality can fall below that of widely spaced plantings if trees become crowded and shading increases (1, 3). Up to 90% of the photosynthetic photon flux density (PPFD) intercepted by citrus trees is absorbed by leaves in the outside meter of the tree canopy (11, 15, 29). Other tree canopies have similar patterns of absorption (14, 17). In hedged peach trees, for example, the greatest absorption of PPFD occurs in the outer 25 cm (16). Differential absorption and light distribution within the canopy results in microclimatic gradients of PPFD, temperature, and evaporative demand (14, 31). Contrasting microclimates within canopies can affect anatomical and morphological characteristics (8, 20) as well as physiological response of leaves (16, 32, 33) and fruit (25, 27, 31). Anatomical differences between sun and shade leaves are well known (7, 8) and leaves of most species will acclimate to changing light environments (2, 9, 22). Leaves produced in high light are thicker (8), have greater specific leaf weight (SLW) (16) and nitrogen content (19), but usually have less chlorophyll content on a weight basis than leaves that are acclimated to shade (13).

Pruning and hedging have been used in citrus production to control tree growth and to reduce yield losses from shading (1, 10, 23) by increasing light penetration into the canopy and thereby modifying bearing surfaces (35). When trees are hedged, leaves that were first produced in full sunlight at shoot tips and gradually were shaded by subsequent growth are once again exposed to full sunlight. Other than physical (20) and nitrogen content (19) differences between sun and shade leaves, little is understood about acclimation of citrus leaves to contrasting light environments. Furthermore, the time course of changes in anatomical, physical, and chemical characteristics that occur in citrus leaves during light acclimation has not been well characterized. This study was therefore designed to compare physical characteristics and the nitrogen and chlorophyll content of citrus leaves grown in and transferred to widely different light regimes. These observations could be used to interpret physiological responses of these leaves in different light environments.

Materials and Methods

Ninety seedlings each of 'Duncan' grapefruit and 'Pineapple' sweet orange were grown in flats in the greenhouse and transplanted when they were 4-months-old into 2 liter pots containing 50% sterilized sand and 50% commercial blend of 3 peat:1 perlite:1 vermiculite (by volume) with added P (4). One-third of each species was kept in full sunlight with a maximum PPFD of 2300 μmol $s^{-1}m^{-2}$, one-third under one layer of 50% shade cloth (V.J. Growers, Apopka, Fla; maximum PPFD = 1100 μmol $s^{-1}m^{-2}$,) and ⅓ under 4 layers of shade cloth (maximum PPFD = 200 μmol $s^{-1}m^{-2}$). Seedlings were watered well under these PPFD treatments for 5 months, from March through July, and were fertilized biweekly with a complete fertilizer (20N–20P–20K + Mg). Leaf temperatures were not monitored, but sun-exposed leaves typically have higher daytime temperatures than shaded leaves (31).

The spectral distribution of wavelengths between 400 and 700 nm in full sunlight and under the shade treatments were characterized in increments of 10 nm using a portable spectroradiometer (modified from a Bausch & Lomb Spectronic mini-20) on a clear day in October. The spectral distribution in full sunlight was comparable to those reported previously (12), and the shade cloth reduced wavelengths equally within this range as reported by Kappel and Flore (16) (data not shown).

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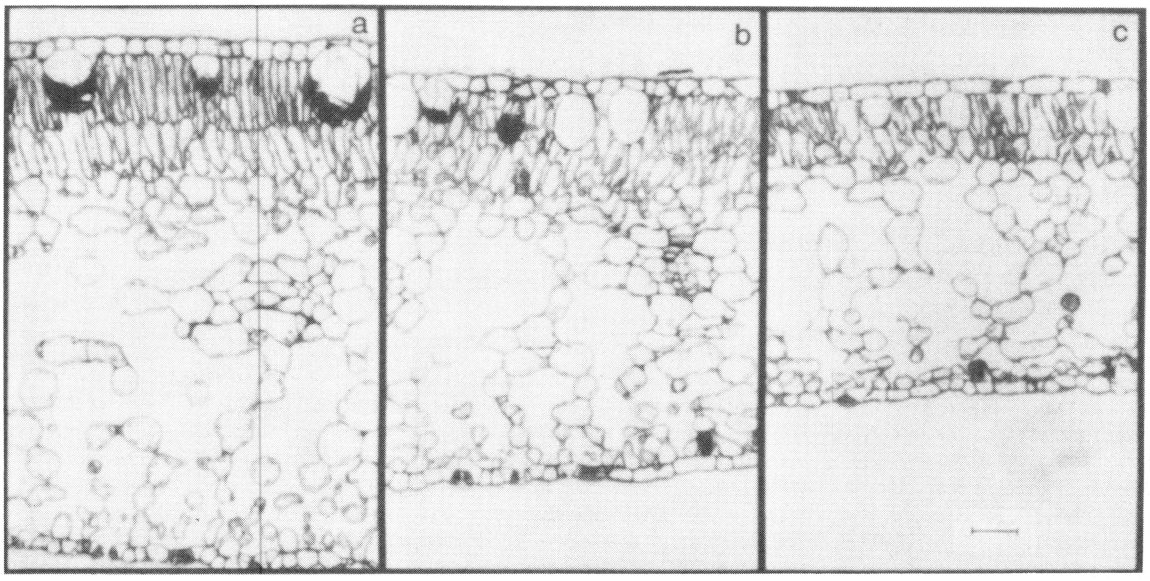

Fig. 1. Light micrographs of cross sections of grapefruit leaves grown under: (**a**) full sunlight, (**b**) 50% shade, and (**c**) 90% shade. Bar = 30 μm.

It takes 6–10 weeks after full expansion for citrus leaves to become fully mature and hardened (30, 33). Since leaf water relations characteristics are known to change during this period (33), care was taken to sample only fully matured leaves. All measurements were made on such leaves which were marked on each 9-month-old seedling. Half of the seedlings of both species in 90% and 50% shade then were transferred to full sunlight to simulate the contrasting light environment that occurs after hedging, and half of the seedlings in full sunlight were transferred to 50% shade to simulate transitions in the light environment that occurs during the course of normal canopy development. This transfer of seedlings resulted in a total of 6 PPFD treatments which consisted of the 3 original growth conditions; high, intermediate, and low PPFD, and the 3 transferred treatments (hereafter referred to as low to high, intermediate to high, and high to intermediate).

Table 1. Mean (± 1 SD, n = 6) physical characteristics of grapefruit leaves grown under high (full sun), intermediate (Int, 50% shade) and low (90% shade) PPFD and the percentage of change of each after being transferred into new PPFD for 12 weeks.

PPFD level	Leaf thickness[z] (mm)	Tissue density[z] (mg mm^{-3})	Air space per leaf vol.[z] (%)
During growth			
High	0.382 a	1.15 a	29.2 c
Int	0.319 b	1.12 b	31.7 b
Low	0.229 c	1.11 b	34.9 a
Transferred[y]		*Change (%)*	
High → Int	−7.1[x]	−1.7[x]	+4.0
Int → High	0	+2.6	−4.1
Low → High	+10.2	+3.5[x]	−6.6

[z]Mean separation within the group by Duncan's multiple range test ($P < 0.05$).
[y]Seedlings were grown under the original PPFD conditions for 5 months prior to being transferred into the new PPFD.
[x]Means used to calculate percent change from corresponding original growth condition were separated by Duncan's multiple range test ($P < 0.05$).

Table 2. Mean (± 1 SD, n = 6) physical characteristics of orange leaves grown under high (full sun), intermediate (Int, 50% shade), and low (90% shade) PPFD, and percentage of change of each after being transferred into new PPFD conditions for 12 weeks.

PPFD level	Leaf thickness[z] (mm)	Tissue density[z] (mg mm^{-3})	Air space per leaf vol.[z] (%)
During growth			
High	0.364[a]	1.15[a]	29.1[b]
Int	0.320[b]	1.13[b]	26.9[c]
Low	0.242[c]	1.12[b]	31.3[a]
Transferred[y]		*Change (%)*	
High → Int	−2.2	−2.6[x]	+5.8
Int → High	−5.9	+1.5	+8.8
Low → High	+5.5	+2.7[x]	−4.5

[z]Mean separation within the group by Duncan's multiple range test ($P < 0.05$).
[y]Seedlings were grown under the original PPFD conditions for 5 months prior to being transferred into the new PPFD.
[x]Means used to calculate percent change from corresponding original growth condition were separated by Duncan's multiple range test ($P < 0.05$).

Six leaves were sampled at 2-week intervals from each group of seedlings for light microscope observations, chlorophyll content, and SLW determinations. Two 1 cm diameter disks were removed from the central area of the lamina (on either side of the midrib) of 3 leaves and used to determine leaf chlorophyll, using N-N dimethyl formamide as a solvent (21). About 1% to 2% of leaf tissue was removed from the central area of the lamina of the 3 remaining leaves with a razor blade and was fixed in 3% glutaraldehyde for 1 hr followed by 2% osmium tetroxide for 2 hr. All fixatives were prepared in 0.2 M potassium phosphate buffer, pH 7.2. The tissue was transferred to 0.2 M phosphate buffer, dehydrated, and embedded in epoxy resin (28) and thin (1 μm) sectioned for light microscopic ob-

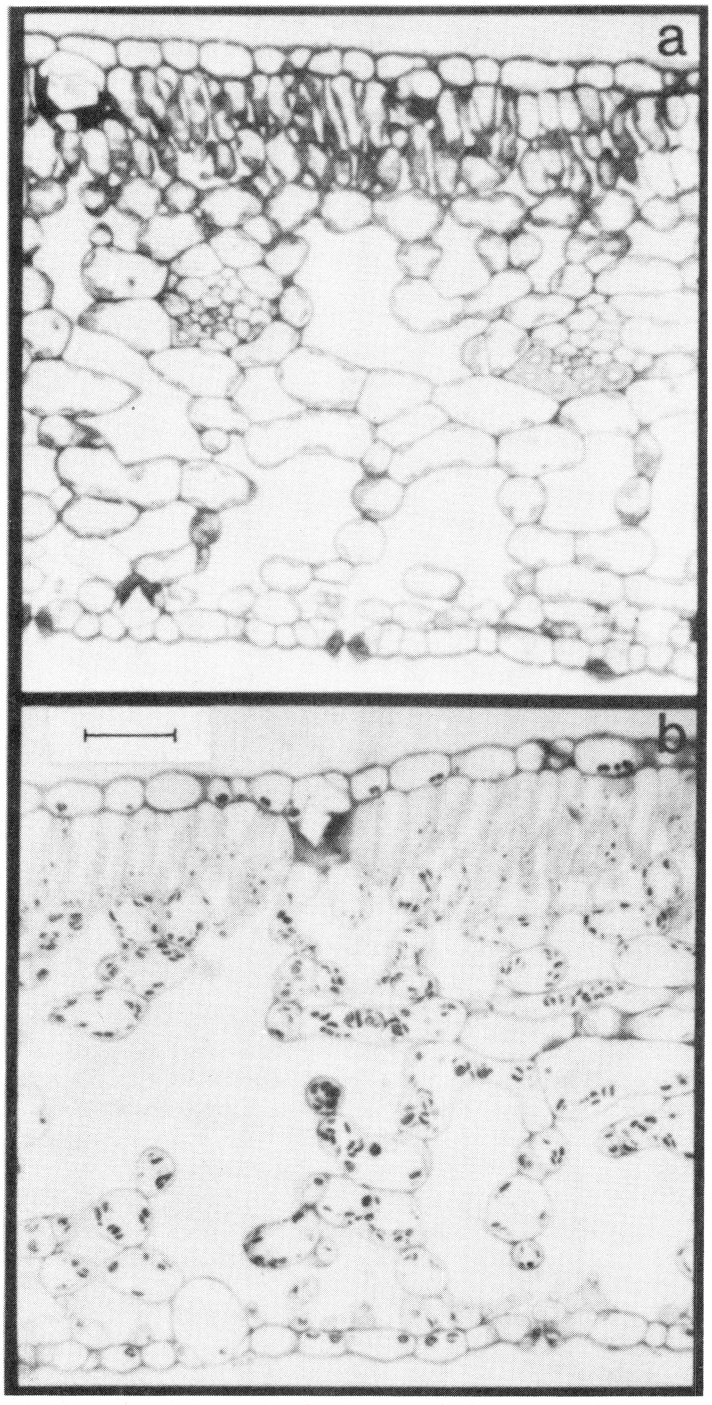

Fig. 2. Light micrographs of cross sections of orange leaves grown under: (**a**) 90% shade, and (**b**) after being transferred into full sunlight for 2 weeks. Bar = 30 μm.

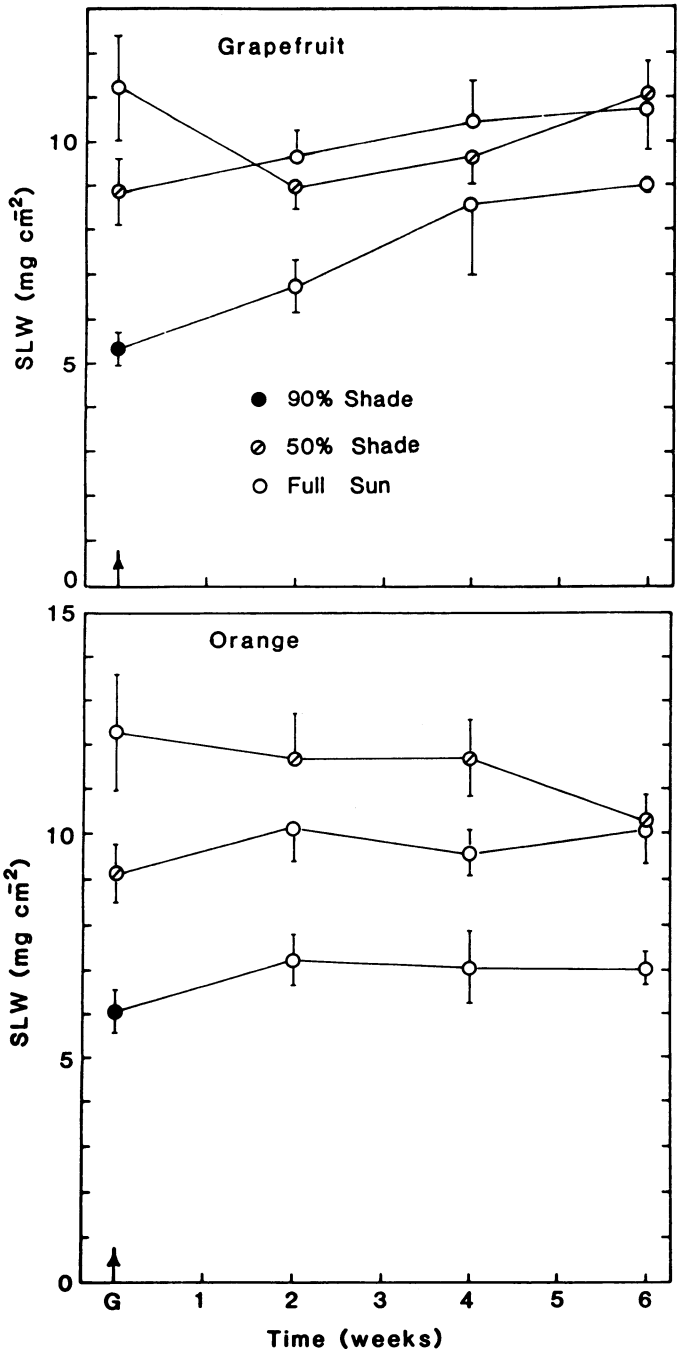

Fig. 3. Specific leaf weight (SLW, $\bar{X} \pm 1$ SD, n = 6) of grapefruit and orange leaves grown (G, arrow) for 5 months under full sunlight, 50% shade, or 90% shade then moved into full sunlight or 50% shade.

servation. Leaf area was determined with a LI-COR leaf area meter (L1-3000), and the leaves were dried at 60°C to a constant weight and weighed for calculating SLW (mg dry weight/cm^2 leaf area). Ten additional leaves within the same age group were sampled and pooled together prior to the PPFD transfers, and at 2 and 4 weeks thereafter for total N determination by Kjeldahl analysis (5). Both N content and SLW from seedlings not moved from the 3 original PPFD were not significantly different through time (tested by analysis of variance) so were pooled into a composite sample for comparison with leaf samples from seedlings that were transferred. Total N and chlorophyll content data were expressed on a leaf area basis.

At the end of the experimental period, 6 seedlings from each PPFD treatment were kept under laboratory PPFD (20 μmol $s^{-1}m^{-2}$) for 1 hr to increase leaf water content to near maximum. One leaf was harvested from each seedling, and its leaf area, fresh weight, fresh weight under water, and infiltrated weight under water were determined. These values then were used to calculate average leaf thickness, volume, density, and percentage of air space using the technique described by Raskin (24).

Table 3. Total N and mean (± 1 SD, N = 6) chlorophyll content of grapefruit and orange leaves grown under high (full sun), intermediate (Int, 50% shade), or low (90% shade) PPFD conditions, and 2, 4, and 6 weeks after being transferred into new PPFD conditions.

Fruit	PPFD conditions		N ($mg\ cm^{-2}$)	Chlorophyll[z] ($\mu g\ cm^{-2}$)
	Growth	Transfer		
Grapefruit				
	High		0.264	41.5 a
		High → Int 2 wk	0.208	44.5 a
		4 wk	0.215	45.8 a
		6 wk	---	56.0 b
	Int		0.217	46.2 a
		Int → High 2 wk	0.194	31.7 b
		4 wk	0.209	37.3 a
		6 wk	---	33.5 b
	Low		0.147	48.7 a
		Low → High 2 wk	0.123	35.4 b
		4 wk	0.179	16.9 c
		6 wk	---	22.9 b
Orange				
	High		0.331	48.5 b
		High → Int 2 wk	0.259	58.2 ab
		4 wk	0.316	60.9 a
		6 wk	---	61.9 a
	Int		0.236	57.1 a
		Int → High 2 wk	0.208	49.9 b
		4 wk	0.269	55.9 a
		6wk	---	50.9 b
	Low		0.144	57.1 a
		Low → High 2 wk	0.152	29.4 c
		4 wk	0.213	35.3 b
		6 wk	---	38.6 b

[z]Values within the group followed by different letters differ significantly ($P < 0.05$) as judged by Duncan's multiple range test.

Data were analyzed using AOV and Duncan's multiple range test at $P < 0.05$.

Results and Discussion

Microscopic observations of leaf cross-sections revealed that leaves grown under high PPFD were thicker and denser than leaves grown under intermediate or low PPFD (Fig. 1). Since there were no qualitative difference between micrographs of the 2 species that could be attributed to growth treatment, only grapefruit leaves are shown. Palisade cells formed 2 distinct layers in sun-grown leaves, but this arrangement was less well-defined in shade leaves. In shade leaves, pigments seem to be more concentrated in the upper tissue layers than in those below. Differences in pigment distribution support the observations of others that shaded leaves tend to have more chlorophyll in the palisade tissues of the leaf (8, 16). This arrangement likely enhances light harvesting efficiency, as leaves from low PPFD also were more horizontal whereas high PPFD leaves appeared somewhat folded along the midvein as previously observed by Monselise (20). This folding could be a high temperature avoidance mechanism or could allow for a smaller leaf profile to enhance light penetration into the canopy. Light micrographs of leaves transferred reciprocally between high and intemediate PPFD revealed very little qualitative changes among these treatments (micrographs not shown). Transferring leaves from low to high PPFD conditions, however, resulted in bleaching or dispersing of the pigments in the pallisade tissue of both species within 2 weeks (Fig. 2). Again, there were no qualitative differences between the micrographs of the 2 species, and only orange micrographs are shown. Pigmentation seemed to be more diffuse or less dense in the low to high PPFD leaves as compared to low PPFD leaves. These microscopic studies support the visual observations of leaf chlorosis in the low to high PPFD plants which is often referred to as sunburn. This response is a temporary one and usually disappears after a period of several weeks, as it did in this study.

Leaves grown in full sunlight had twice the SLW as that of low PPFD leaves, whereas leaves grown in 50% shade were intermediate (Fig. 3). The SLW of the 2 species within each of the 3 original growth PPFD did not differ significantly. Both species responded similarly to changing PPFD. There was a general response of SLW, increasing initially in full sunlight or decreasing in 50% shade. After 6 weeks, SLW of high to intemediate and intermediate to high PPFD of both species was not different, but the SLW of grapefruit low to high PPFD increased much more than that of low to high orange leaves. Such responses could have been due to species differences in leaf area, as grapefruit tends to have larger leaves.

Determining the average leaf thickness from the total volume of a leaf of known area results in estimates (Tables 1, 2) consistently 8% to 9% greater than those measured on the micrographs (Fig. 1, 2). Nonetheless, the relative differences between treatments are consistent. Since the volume/area technique included the entire leaf along with the relatively thick midvein,

this method may have resulted in somewhat greater and perhaps more accurate estimates of average leaf thickness than obtained from micrographs.

Differences in leaf thickness and leaf density with respect to original PPFD during growth, and changes in these leaf characteristics after transferring to new PPFD conditions (Table 1, 2) support the SLW data (Fig 3). Leaves of both species grown in high PPFD were significantly thicker and their tissues denser than leaves grown under medium or low PPFD. Again, there is a tendency for grapefruit leaves to respond more dramatically to changing PPFD than orange leaves. Furthermore, low PPFD leaves have a higher percentage of air space within leaf tissues than medium or high PPFD leaves. Although leaf density changes significantly in response transferring into new PPFD, average leaf thickness does not, except for high to intermediate grapefruit leaves (Table 1). These results, along with the small inconsistent changes in percentage of air space, show that increases in SLW (weight per area) in low to high PPFD leaves are due to increases in the density (weight per volume) of existing tissue and not due to the addition of new tissue. The conservative nature of percentage of air space is an important consideration in interpreting changes in physical conductances to diffusion of CO_2 and water vapor.

Leaf total N content (area basis) was highest in high PPFD leaves and lowest in low PPFD leaves (Table 3). Nitrogen content was positively correlated ($r = 0.86$) with SLW. These data confirm previous observations (19) that citrus leaf N is highest in sun-exposed leaves. With so few N samples, it is difficult to draw strong conclusions, but leaf N content tends to drop within 2 weeks after transferring into new PPFD regardless of PPFD regimes. In this respect, changes in leaf N content did not necessarily parallel changes in SLW. The reduction in leaf N occurred more quickly than changes in SLW and was apparently temporary, because leaf N generally increased between 2 and 4 weeks. Similarly, chlorophyll content (area basis) of low to high PPFD leaves of both species decreased after 2 weeks but began to recover significantly after 4 weeks in orange leaves and after 6 weeks in grapefruit leaves. This decrease and recovery also supports the previously described visual observations of temporary bleaching in low to high PPFD leaves. Total chlorophyll content continued to increase in the high to medium PPFD leaves of both species, but decreased temporarily in the medium to high PPFD leaves.

The anatomical, physical, and chemical characteristics of citrus leaves in response to maximum light levels during growth, indicate how citrus leaves can acclimate to different conditions in the canopy. The changes noted in leaf characteristics during light acclimation indicate that citrus leaves can acclimate to changes in growth conditions, even after leaves are fully mature. These responses are analogous to changes that might occur during canopy development and hedging and may be more dramatic than those reported for other tree fruit species, such as peaches (16). This difference may be related to the relatively long lived (up to 3 yr) evergreen leaves of citrus. Differences between grapefruit and orange leaves may be related to the fact that grapefruit trees generally are larger than orange trees. Leaf area index increases and PPFD penetration decreases as trees grow (15). Grapefruit leaves therefore must acclimate to deeper shade conditions than orange leaves.

Highest SLW, leaf tissue density, and N content were positively correlated with highest PPFD during growth and likely reflected enhanced physiological activity under high PPFD conditions. There is no doubt that increased light penetration into hedged canopies stimulates leaf and fruit production in interior canopy positions. It is possible that temporary decreases in nitrogenous compounds, photosynthates and nonstructural carbohydrates in response to changing PPFD conditions, were responsible for decreases in SLW and tissue density (26). Relatively long term increases in leaf density also may have been due to increases in photosynthates and/or due to the conversion of carbohydrates and nitrogen compounds into structural tissue components.

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Light Acclimation in Citrus Leaves. II. CO_2 Assimilation and Light, Water, and Nitrogen Use Efficiency

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Additional index words. grapefruit, orange

Abstract. **Net CO_2 assimilation (A) rates of 'Duncan' grapefruit (*Citrus paradisi* Macf.) and 'Pineapple' orange (*C. sinensis* L.) seedlings grown under 3 different photosynthetic photon flux densities (PPFD), were measured in an open gas exchange system under controlled environmental conditions. Apparent quantum yield (ø), mesophyll conductance to CO_2 (G_m), leaf conductance to H_2O vapor (G_l), transpiration (E) and water use efficiency (WUE) also were examined. Leaves of both species grown under high PPFD (full sunlight) had the greatest maximum rates of A, but the low PPFD (90% shade) leaves had the highest ø. The WUE of low PPFD grapefruit leaves was less than that of the high PPFD leaves but increased within 2 weeks after being moved into full sunlight. Transferring seedlings from low to high PPFD decreased ø of grapefruit but not of orange leaves. Changes in A were more strongly correlated to G_m than to G_l. Carbon dioxide assimilation rate was positively correlated to total leaf nitrogen content. Citrus leaf photosynthetic characteristics and resources use efficiency not only acclimate to the light regimes under which they expand and mature, but leaves are capable of acclimating to new light regimes, even after full maturation.**

Bjorkman (2) recently has reviewed how leaves acclimate to changes in the radiation environment to maximize photosynthetic efficiency under a particular set of conditions. Leaves growing in full sunlight are not only thicker with more densely packed mesophyll (4, 19) than leaves growing in shade, but also have higher light-saturated CO_2 assimilation rates (A) (1, 7, 11, 20, 22). Furthermore, sun leaves have higher nitrogen use efficiency than shade leaves, as estimated by expressing A on a total leaf nitrogen (N) basis, A/N (5, 6). Although citrus leaves from exterior canopy positions have higher N contents than leaves from interior positions (15), there is no report of citrus nitrogen use efficiency. Such information can provide insight regarding resource partitioning (3, 9, 23) during acclimation in tree canopy microclimates.

Shade leaves typically have increased quantum yield (ø), an estimate of quantum use efficiency during CO_2 fixation, as shown by greater initial slopes in the quantum yield region of the A vs. photosynthetic photon flux density (PPFD) response curve (1, 24). High ø is, of course, an important advantage in shaded environments (27). Since the majority of leaves in a tree canopy are growing under reduced light, higher ø of shade leaves allows them to capitalize on existing light microclimates (18). Although the plasticity of ø in sun and shade leaves has been described for many crops (20, 24) native shrubs and trees (1, 8, 20), there is no available information on how ø varies with the PPFD environment of citrus trees. This relationship can

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