Photosynthetic Responses of Container-grown *Illicium* L. Taxa to Sun and Shade

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ABSTRACT. Illiciums, or star-anises, have increased in popularity in the nursery and landscape industries. However, confusion exists as to which taxa are tolerant of high light intensities during production and subsequent establishment in the landscape. We investigated the effect of two light intensity treatments, 45% and 100% full sunlight, on gas-exchange parameters of five *Illicium* taxa: *Illicium anisatum* L., *I. floridanum* Ellis. ‘Pebblebrook’, *I. henryi* Diels., *I. lanceolatum* A.C. Sm., and *I. parviflorum* Michx. Ex. Vent. ‘Forest Green’. Light-response curves were determined for individual leaves, and mean response parameters calculated. Chlorophyll and total carotenoids were analyzed after extraction in acetone, with total chlorophyll also estimated with a SPAD chlorophyll meter. In general, highest rates of CO₂ assimilation ($A_{\max}$) and lowest rates of dark respiration (R_d) were found in the 45% light treatment for all taxa. Both *Illicium anisatum* and *I. floridanum* ‘Pebblebrook’ had substantial reductions in $A_{\max}$ in 100% light, 94% and 81% respectively, compared to plants grown in the 45% light treatment. *Illicium henryi* failed to survive the 100% light treatment. *Illicium lanceolatum* and *I. parviflorum* ‘Forest Green’ were least affected by the 100% light treatment. Severe photooxidative bleaching was noted and confirmed by SPAD and pigment data, although SPAD readings were a poor predictor of total chlorophyll. For taxa of *Illicium* in our study, photosynthetic gas-exchange parameters and foliage pigment characteristics were improved in the low light treatment, suggesting optimal growth occurs in shaded conditions.

The genus *Illicium* [Illiciaceae (de Candolle) A.C. Smith] is native to subtropical and temperate regions of southeastern Asia, the Malay archipelago, southeastern United States, Mexico, and the Caribbean (Qi, 1995; Smith, 1947). In the past decade, Illiciums (star-anises) have become increasingly popular ornamentals for landscape use. Ease of propagation, lack of pests and diseases, and durability in the landscape and nursery production have led to their widespread use in the landscape industry (Dirr, 1986; Fantz et al., 1991). Increased demand has prompted many nurseries to seek out new *Illicium* species and forms to introduce to the nursery trade, often before best cultural practices have been established.

There are conflicting views as to the capability of various *Illicium* species to survive in full sun. Fantz et al. (1991) suggested that cultivated *Illicium* species grow well and flower more profusely in full sun than in shade. However, Dirr (1993; 1998) observed color loss in foliage of plants when grown in full sun. A distinct yellowing or bleaching of foliage in high light intensities is one symptom of prolonged photoinhibition resulting from photooxidation of plant pigments (Minkov et al., 1999; Xu and Shen, 1999). Photoinhibition is an adaptive process, whereby plants regulate electron transport and energy dissipation in times of excessive excitation of their photosynthetic apparatus (Long et al., 1994). The xanthophyll cycle plays the primary role in thermal energy dissipation, and like other sun-shade acclimations, responds to differences in light intensities. Sun-tolerant or high light tolerant plants exhibit greater concentrations of xanthophyll cycle components, and carotenoids in general, than shade-

adapted species, and likewise, sun leaves contain greater concentrations of these carotenoids than leaves developed in low light on the same plant (Demmig et al., 1987; Demmig-Adams et al., 1989; Demmig-Adams et al., 1995; Demmig-Adams, 1998; Thayer and Björkman, 1990).

The range of light intensity to which a plant can acclimate is determined by an individual species genetic adaptation to the light environment of its native habitat (Boardman, 1977; Pearcy, 1998). Numerous changes in leaf morphology, physiology, and biochemistry are required for acclimation of photosynthesis to various light intensities (Björkman, 1981; Boardman, 1977). Plants native to high light environments are capable of higher photosynthetic rates at high-light intensities than plants from low-light environments. Sun plants are able to increase light-saturated photosynthetic capacity by increasing protein synthesis, Rubisco activity, and components of the electron-transport chain. Shade plants have inherently low photosynthetic rates, and lack the ability to effectively increase light-saturated photosynthesis (Björkman, 1981).

Illiciums are generally understory shrubs or sub-canopy trees in their native habitats (Gibson, 1992; Nitta and Ohsawa, 1997; White and Thien, 1985), suggesting photosynthetic responses indicative of shade-adapted species. Genetic adaptations for survival in low light intensities may preclude sufficient acclimation by Illiciums when grown in high light intensities. Therefore, our objectives were 1) to quantify the photosynthetic responses of various *Illicium* taxa to two light intensity treatments, and 2) to determine if photoinhibition and photooxidation occurs in Illiciums grown in high light intensities.

Materials and Methods

Five *Illicium* taxa, *I. anisatum*, *I. floridanum* ‘Pebblebrook’, *I. henryi*, *I. lanceolatum*, and *I. parviflorum* ‘Forest Green’, currently available in the nursery industry were studied. Terminal cuttings were taken from plants growing at the Coastal Plain Experiment Station, Tifton, Ga., on 20 Sept. 1999 and transported to Wight Nurseries, Cairo, Ga., for propagation. Well-rooted liners

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were transported to the Coastal Plain Experiment Station, where they were potted into 2.8-L black plastic containers on 22 May 2000. The substrate consisted of an 8 milled pine bark : 1 sand mix (by volume) amended with dolomitic lime at $1.2 \text{ kg}\cdot\text{m}^{-3}$ and Osmocote Plus 15.0N–4.0P–9.9K (Scotts Co., Marysville, Ohio) applied as a top-dressing with N at $1.2 \text{ kg}\cdot\text{m}^{-3}$ (20.2 g/container). Plants were randomly placed in one of two light intensity treatments, either 100% or 45% ambient photosynthetic photon flux (*PPF*), in a randomized split-plot design. Plants in 100% *PPF* were grown in full sun on a nursery container pad, where average daily maximum ambient *PPF* was $2110 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants in 45% *PPF* were grown in hoop houses covered in black woven polypropylene fabric where average daily maximum ambient *PPF* was $1010 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$. Plants were watered as needed.

Beginning in July, plants with one flush of growth hardened under either of the two light treatments were transported to Athens, Ga., for gas-exchange measurements. Plants were placed under the same light treatments in Athens under similar nursery conditions and were brought into the laboratory between 0600 and 0700 HR and allowed to acclimate one hour before measurements began. The container substrate was fully hydrated the night before measurements were performed. Gas-exchange measurements were made using a portable photosynthesis system (LI-6200; LI-COR, Lincoln, Nebr.) with a 250-mL leaf chamber. A LED lighting system (QB6200; Quantum Devices, Barneveld, Wis.) attached to the top of the leaf chamber provided light for all measurements. A metal halide light provided supplemental light (between 350 and $700 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPF*) to the remaining plant during the single leaf measurements. Measurements were determined on a fully expanded, mature leaf below the terminal bud on hardened new growth. Measurements were made at 0, 30, 80, 150, 250, 350, 450, 600, 900, 1200, 1500, and $2000 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPF*. The LED lighting system was calibrated with a quantum radiometer-photometer (LI-189; LI-COR) to attain the desired increment *PPF* levels. Leaf chamber CO_2 concentration was maintained at $365 \pm 10 \text{ mg}\cdot\text{L}^{-1}$ and leaf temperatures were between 25 and 30°C . Because of low relative humidity in the laboratory (40%) and low photosynthetic rates of *Illicium*s, leaf chamber relative humidity was low resulting in vapor pressure deficits (VPDs) of $2.0 \pm 0.5 \text{ kPa}$.

After the final gas-exchange measurement, the leaf area enclosed in the chamber was measured using a portable area meter (LI-3000; LI-COR). A SPAD-502 chlorophyll meter (Minolta, Ramsey, N.J.) was used as a non-destructive tool for estimating leaf chlorophyll (Markwell et al., 1995). Two readings per leaf were taken midway between the leaf mid vein and margin and averaged.

For pigment analysis, one 13-mm leaf disk per leaf was punched out and fresh weight recorded. Leaf disks were stored at -80°C until

pigment analyses were performed. Chlorophylls *a* and *b*, and total carotenoids were extracted using 80% acetone following the methods of Bruinsma (1963) with the following exceptions. Because of poor extraction after 24 h in the dark at 4°C , leaf disks were homogenized in the acetone solution and extracted for another 24 h in the dark at room temperature and centrifuged at $2000 g_n$ for 2 min. The extinction of the supernatant was measured with a spectrophotometer (Spectronic Genesys 5, Spectronic Instruments, Rochester, New York) at 470, 646, and 663 nm using the specific absorption coefficients of Lichtenthaler and Wellburn (1983).

Individual photosynthetic-response curves were analyzed by nonlinear regression (SigmaPlot 4.0 for Windows, SPSS, Chicago, Ill.). Cardinal points were calculated from the fitted equations or taken directly as data points. Dark respiration (R_d) was measured at $0 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPF* and maximum net CO_2 assimilation (A_{max}) was the highest measured rate of net CO_2 assimilation (A_{net}) for each plant. The photosynthetic saturation point (A_{sat}) was estimated as 95% of A_{max} (Norcini et al., 1991). Apparent quantum yield (Φ_i) and light compensation points (A_0) were calculated by fitting data for A_{net} from *PPF* $< 150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to a linear regression, with *PPF* as the independent variable (Leverenz, 1987), where the slope of the linear regression function equals Φ_i and the light compensation point is $A_{\text{net}} = 0$. Data were analyzed as a split plot design using a general linear model (PROC GLM; SAS version 8.0 for Windows, Cary, N.C.). Light transmittance was the main plot with an error term of block $\times$ light. Taxa was the subplot factor with an error term of block $\times$ taxa + block $\times$ taxa $\times$ light. Standard error of difference between two means (SED) was calculated for all treatment combinations. The relationships between total chlorophyll (Chl_{tot}) and SPAD data were analyzed using regression analysis.

Results

A significant light $\times$ taxa interaction ($P < 0.05$) occurred for each photosynthetic and pigment parameter except A_0 and F_i (data not shown). The light compensation point (A_0) and Φ_i were

Fig. 1. Photosynthetic light response curves for *Illicium anisatum* grown in 45% (○) and 100% (●) of full sunlight. Measurements were made at $365 \pm 10 \text{ mg}\cdot\text{L}^{-1} \text{ CO}_2$, leaf temperatures between 25 and 30°C , and a vapor pressure deficit of $2.0 \pm 0.5 \text{ kPa}$. Negative photosynthetic rates beyond $150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ *PPF* for plants grown in 100% light precluded comparison of quantum yields (Φ_i) and light compensation points (A_0) between treatments. Data points represent means, with $n = 6$. Error bars represent standard errors for the means.

Table 1. Photosynthetic gas-exchange parameters for five *Illicium* taxa grown in 100% and 45% of ambient photosynthetic photon flux. Mean of six replications except *I. floridanum* ‘Pebblebrook’ in 45% light where n = 5.

Taxon	Light level (%)	Photosynthetic gas-exchange parameters ^z				
		A _{max}	A _{sat}	R _d	A ₀ ^y	Φ _I ^y
		(μmol CO ₂ /m ² ·s ⁻¹)			(μmol photons/m ² ·s ⁻¹)	
<i>I. anisatum</i>	100	0.51	0.48	-2.11	---	---
	45	8.39	7.97	-0.78	22.2	0.0261
<i>I. floridanum</i> ‘Pebblebrook’	100	1.55	1.47	-1.19	---	---
	45	7.48	7.11	-1.33	56.6	0.0202
<i>I. henryi</i> ^x	100	---	---	---	---	---
	45	3.05	2.90	-1.05	57.9	0.0146
<i>I. lanceolatum</i>	100	3.78	3.59	-2.07	81.9	0.0197
	45	5.67	5.38	-1.81	55.9	0.0295
<i>I. parviflorum</i> ‘Forest Green’	100	9.07	8.62	-1.20	29.4	0.0330
	45	10.90	10.37	-0.61	16.1	0.0327
SED ^w						
Between light treatments, same taxa		0.73	0.70	0.30	---	---
Between taxa, same light treatment		0.76	0.72	0.31	---	---

^zMaximum net leaf CO₂ assimilation = A_{max}, net leaf CO₂ assimilation at light saturation = A_{sat}, dark respiration = R_d, light compensation point = A₀, and apparent quantum yield of leaf photosynthesis = Φ_I.

^yA₀ and Φ_I were not calculated for *I. anisatum* and *I. floridanum* ‘Pebblebrook’ grown in the 100% light treatments due to severe inhibition of photosynthesis at the low light levels used for calculation of these parameters.

^xNo *I. henryi* survived the 100% light treatment.

^wStandard error of difference between two means (SED). No significant interaction or light effect was observed for A₀ and Φ_I. A significant (*P* < 0.001) taxa effect occurred for both parameters. SED for taxa comparison are 6.5 and 0.00265 for A₀ and Φ_I, respectively.

not calculated for *I. anisatum* and *I. floridanum* ‘Pebblebrook’ grown in the 100% light level treatment because of negative photosynthetic rates at the low light levels (<150 μmol·m⁻²·s⁻¹ PPF) used for calculation of these response variables, as shown in Fig. 1. Light had no effect on Φ_I and A₀; however, there was a significant (*P* < 0.001) taxa effect for both parameters (data not shown).

In general, the highest A_{max} values for each taxa studied occurred in the 45% light treatment (Table 1). Although A_{sat} varied by taxa and light treatment, saturation of photosynthesis occurred at similar intercellular CO₂ (C_i) levels, between 200 and 230 mg·L⁻¹ (data not shown). However, plants of *I. anisatum* and *I. floridanum* ‘Pebblebrook’ in 100% light that exhibited inhib-

ited photosynthetic rates, saturated at higher C_i levels, between 300 and 350 mg·L⁻¹ (data not shown).

No plants of *I. henryi* survived the 100% light treatment, and *I. henryi* plants in the 45% light treatment had low A_{max}, A_{sat}, and Φ_I relative to the other taxa in the 45% light treatment (Table 1). Dark respiration (R_d) was also low, and thus the low Φ_I was the main contributing factor to the high A₀ for shade plants of *I. henryi*.

Illicium anisatum and *I. floridanum* ‘Pebblebrook’ had similar responses to light treatments (Table 1). For both species in the 100% light treatment, A_{max} and A_{sat} were greatly reduced compared to rates in the 45% light treatment. Maximum rates of net CO₂ assimilation (A_{max}) decreased by 94% and 81% for *I. anisatum* and *I. floridanum* ‘Pebblebrook’, respectively. Dark respiration rates varied between

Table 2. Leaf pigment data for five *Illicium* taxa grown in 100% and 45% ambient photosynthetic photon flux. Mean of six replications except *I. floridanum* ‘Pebblebrook’ in 45% light where n = 5.

Taxon	Light level (%)	Leaf pigment concn ^z (μg·cm ⁻²)					
		Chl _{tot}	Chl _a	Chl _b	Chl _{a:b}	Chl _{x+c}	SPAD
<i>I. anisatum</i>	100	47.0	17.9	29.1	0.61	9.8	17.5
	45	85.1	32.2	53.0	0.61	2.3	65.7
<i>I. floridanum</i> ‘Pebblebrook’	100	83.8	31.9	51.9	0.61	17.3	27.8
	45	56.8	22.2	34.6	0.64	7.6	59.8
<i>I. henryi</i> ^y	100	---	---	---	---	---	---
	45	51.5	23.9	27.6	0.87	6.3	51.5
<i>I. lanceolatum</i>	100	64.6	26.8	37.8	0.71	7.5	46.9
	45	55.3	25.6	29.7	0.85	4.2	58.9
<i>I. parviflorum</i> ‘Forest Green’	100	38.3	14.5	23.8	0.60	4.0	54.8
	45	35.5	13.0	22.5	0.58	2.7	57.8
SED ^w							
Between light treatments, same taxa		8.1	3.5	4.7	0.04	1.7	8.6
Between taxa, same light treatment		8.2	3.6	4.8	0.04	1.8	4.2

^zAbbreviations: total chlorophyll (Chl_{tot}), chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), chlorophyll *a:b* ratio (Chl *a:b*), total xanthophylls and carotenoids (Chl_{x+c}), SPAD-502 chlorophyll meter reading (SPAD).

^yNo *Illicium henryi* survived the 100% light treatment.

^wStandard error of difference between two means (SED).

species, from -2.11 ± 0.36 and $-1.19 \pm 0.17 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, for *I. anisatum* and *I. floridanum* 'Pebblebrook', respectively. Both species had comparable rates of A_{max} and A_{sat} in the 45% light treatment. *Illicium anisatum*'s high Φ_i and low R_d contributed to a low A_0 . *Illicium floridanum* 'Pebblebrook's low Φ_i and high R_d resulted in a high A_0 .

Illicium lanceolatum and *I. parviflorum* 'Forest Green' can also be grouped together according to their similar responses to the light treatments, even though photosynthetic rates differed (Table 1). Maximum rates of net CO_2 assimilation (A_{max}) and A_{sat} decreased by 33% and 17% for *I. lanceolatum* and *I. parviflorum* 'Forest Green', respectively, in the 100% light treatment compared with the 45% light treatment. A low Φ_i and high R_d led to a high A_0 for *I. lanceolatum* in the 100% light treatment. In the 45% light treatment Φ_i was higher and R_d remained high, leading to a relatively high A_0 for *I. lanceolatum*. *Illicium parviflorum* 'Forest Green' maintained a high Φ_i in both light treatments. Increased R_d resulted in a higher A_0 for *I. parviflorum* 'Forest Green' in the 100% light treatment. Leaves of *I. parviflorum* 'Forest Green' in 100% PPF had vertically disposed leaves, much more so than on leaves of plants in 45% PPF. This response was not observed in the other *Illicium* taxa.

No consistent pattern was observed in Chl_{tot} due to light treatments (Table 2), which is not uncommon in light intensity studies (Percy, 1998). Chlorophyll $a : b$ ratios were low and remained within a narrow range of 0.58 to 0.87 between light treatments and taxa (Table 2). In general, carotenoid levels increased in the 100% light treatment for all taxa. *Illicium anisatum* and *I. floridanum* 'Pebblebrook' demonstrated the greatest percent increases in carotenoid concentrations of 326% and 127%, respectively. *Illicium lanceolatum* and *I. parviflorum* 'Forest Green' showed the smallest increases of 78% and 42%, respectively. In the 45% light treatment, plants of *I. floridanum* 'Pebblebrook' and *I. henryi* had higher levels of carotenoids relative to other taxa. Total chlorophyll concentrations were poorly fitted to SPAD readings ($R^2 = 0.03$), but did confirm visual observations of foliage color during the experiment. Plants of *I. anisatum* and *I. floridanum* 'Pebblebrook' in the 100% light treatment appeared bleached and yellow, as shown in their low SPAD readings and high carotenoid levels (Table 2). Severe bleaching was observed on plants of *I. henryi* subsequent to plant death in the 100% light treatment. SPAD readings for *I. lanceolatum* were lower in the 100% treatment than in the 45% treatment. Light treatment did not influence SPAD readings of *I. parviflorum* 'Forest Green'.

Discussion

Maximum rates of net CO_2 assimilation (A_{max}) observed for *Illicium* taxa in this study are similar to rates reported for broad-leaf evergreen species adapted to low light environments (Andersen et al., 1991a, 1991b; Langenheim et al., 1984) although these rates may have been somewhat attenuated due to the higher than expected VPD in the leaf chamber during gas-exchange measurements. Low rates of CO_2 assimilation in shade-adapted plants are not attributed to differences in rates of stomatal conductance between sun and shade plants (Björkman, 1981). The inability of shade-adapted species to increase rates of net CO_2 assimilation when grown in high light is also not attributable to stomatal limitations. Langenheim et al. (1984) showed that for several species of tropical shade-tolerant evergreens, stomatal conductance decreased in high light; however, C_i remained similar between light treatments. They suggested that low photosynthetic capacity, rather than low stomatal conductance, resulted in a lack

of photosynthetic acclimation to increases in PPF. A similar trend was observed for *Aucuba japonica* 'Variegata', a shade-adapted, broad-leaved evergreen native to temperate Asia, in a container-production study in Florida (Andersen et al., 1991a). Saturation of *Illicium* taxa in our study occurred from 200 to 230 $\text{mg}\cdot\text{L}^{-1} C_i$, regardless of light treatment and taxa. This C_i level for A_{sat} implies that the inability of *Illicium* taxa in this study to increase A_{max} when grown at 100% light is due to inherently low photosynthetic capacities. The failure to increase rates of photosynthesis with increasing light is a direct result of an inability to increase rate-limiting steps of photosynthesis, including Rubisco synthesis and activation (Seemann, 1989) and electron transport (Björkman, 1981; Boardmann, 1977).

Excess light, or light stress, is induced when the ratio of photon flux density to photosynthesis is high (Demmig-Adams and Adams, 1992). Thus, for plant species unable to increase A_{max} with increases in light, long-term exposure to high light will result in prolonged light stress and photoinhibition, the decrease in photosynthetic activity induced by light in excess of that used in photosynthesis (Xu and Shen, 1999). Substantial decreases in photosynthetic activity were observed for most *Illicium* taxa in the 100% light treatment. The smallest decline in A_{max} (17%) was observed with *I. parviflorum* 'Forest Green'. In addition, F_i , a measure of photosynthetic efficiency which often declines with light stress (Long et al., 1994; Percy, 1998), remained unchanged between light treatments for *I. parviflorum* 'Forest Green', suggesting this taxon was able to avoid light stress. The vertical leaf orientation of plants in 100% light may have effectively decreased the absorption of incident light, possibly to levels observed by plants in the 45% light treatment, a strategy used by mangrove species to avoid high levels of incident PPF (Lovelock and Clough, 1992), and implied here by the low A_0 values plants grown in 100% light. Although photosynthesis appeared to acclimate to high light for *I. parviflorum* 'Forest Green', R_d increased by 97% in high light, suggesting increased maintenance costs, perhaps from increased protein turnover in high light (Percy, 1998). Increased respiration, without an increase in photosynthesis, would have a negative effect on carbon-use efficiency, suggesting optimal growth for *I. parviflorum* 'Forest Green' would occur in light intensities below 100% light.

The decline in A_{max} for *I. lanceolatum* in the 100% light treatment was accompanied by a decline in Φ_i and increased levels of carotenoids. Declines in photosynthesis due to photoinhibition are the result of declines in photosynthetic efficiency, as energy from absorbed quanta is dissipated as heat instead of being used in photochemistry (Long et al., 1994). The xanthophyll cycle is recognized as the major thermal energy dissipation pathway in plants (Long et al., 1994; Xu and Shen, 1999) with increases in total carotenoid concentrations in high PPF due to increases in xanthophyll cycle components (Demmig et al., 1987; Demmig-Adams, 1998; Demmig-Adams et al., 1989; Demmig-Adams et al., 1995; Thayer and Björkman, 1990). However, shade-adapted species have a low capacity for xanthophyll cycle mediated energy dissipation compared to sun-adapted species (Demmig-Adams et al., 1995), and when combined with their low rates of photosynthesis, predispose shade-adapted plants to photoinhibition. Prolonged inhibition in the transfer of excitation energy from excited chlorophyll to the quinnone acceptors results in triplet chlorophyll formation, which reacts with oxygen to produce singlet oxygen and oxygen radicals. Both are active oxygen species capable of damaging proteins, pigments, and

thylakoid membranes, which results in photooxidative bleaching (Minkov et al., 1999). The responses of *I. anisatum* and *I. floridanum* 'Pebblebrook' to 100% light is indicative of this type of severe damage to the photosynthetic apparatus. Both species exhibited significant decreases in $A_{\max}$, and Φ_i decreased to immeasurable rates. Intercellular CO_2 levels remained high, decreasing little below ambient CO_2 levels, indicating a reduced demand for carbon. A more significant decrease in C_i would be expected if the decrease in $A_{\max}$ was due to any decreases in stomatal conductance from the higher than ideal VPD in the leaf chambers during gas-exchange measurements. The observed decreases, however, can occur if there is a massive accumulation of damaged reaction centers, which instead of transferring absorbed light energy for use in carbon assimilation, dissipate absorbed energy as heat (Percy, 1998).

The SPAD readings and increases in carotenoids concentrations confirmed visual observations of photooxidative bleaching in leaves of 100% light grown *I. anisatum* and *I. floridanum* 'Pebblebrook' plants. However, the chlorophyll pigment data are inconsistent with regard to expected chlorophyll losses from photooxidation. *Illicium anisatum* had substantially lower Chl_{tot} combined with increased carotenoids in 100% PPF, corroborating evidence for photooxidative bleaching. *Illicium floridanum* 'Pebblebrook', on the other hand, had high Chl_{tot} , but low SPAD readings in 100% light. These inconsistencies led to the poor relationship between SPAD and chlorophyll data. Campbell et al. (1990) showed that growing conditions affect the relationship of SPAD readings to total chlorophyll, due in part to differences in leaf morphology. In a recent study, SPAD readings were highly correlated to total chlorophyll levels and visual observations of color for greenhouse grown st. augustinegrass, but correlated poorly in field grown plants due to a lack of uniformity in ontogenetic age of the samples and sampling error (Rodriguez and Miller, 2000). Re-analysis of our data, attempting to account for the above possibilities, failed to improve the relationship of SPAD readings to chlorophyll data. The low $\text{Chl } a : b$ ratios observed for *Illicium* taxa in this study are substantially lower than published ratios for other broad-leaved evergreen taxa (Demmig-Adams, 1998; Thompson et al., 1992) and C_3 plants in general (Demmig-Adams, 1998). These low ratios may be indicative of poor extraction of chlorophyll by acetone in *Illicium* leaves, and would also confound the relationship of SPAD readings to chlorophyll pigment data.

Failure of *I. henryi* to survive the 100% light treatment represents the most severe example of the inability to acclimate to high light by a shade-adapted species. Plants were visibly bleached and necrotic within 1 month, and all were dead by the end of the second month. In a light intensity study with *Rhododendron* x 'Pink Ruffles', Andersen et al. (1991b) suggested that photoinhibition and photooxidation damage was responsible for reduced growth and chlorosis of plants in 100% sunlight. They concluded *Rhododendron* x 'Pink Ruffles' required partial shade, with no amount of acclimation preventing chlorosis and dieback when plants were transplanted from various light intensities into full sun. In a similar study using the broad-leaved evergreen *Aucuba japonica* 'Variegata', plants grown in 100% sun became chlorotic and necrotic in just 30 d, with complete defoliation occurring by the end of the summer (Andersen et al., 1991a). *Aucuba japonica* 'Variegata' was classified as a shade obligate, where optimum plant growth occurs in light intensities of less than 47% of full sun. Although *I. henryi* was the only taxon in our study that failed to survive the 100% light treatment, it is highly

probable that *I. anisatum* and *I. floridanum* 'Pebblebrook' would fail to survive the rest of the growing season in full sun, given their poor acclimation by mid-season. High temperature and excess light often occur together in nature, where heat induced disruption of the thylakoid membrane can impair the ability of the leaf to dissipate excess absorbed light (Al-Khatib and Paulsen, 1989). Plants grown in 100% of full sunlight would have been exposed to a combination of high light and high temperatures during the growing season. Our experimental design precluded the partitioning of damage between excess light absorption and differences in foliage temperature expected between the 45% and 100% light treatments.

The photosynthetic responses of *Illicium* taxa reflected the light levels prevalent in their native habitats. *Illiciums* are generally understory shrubs or sub-canopy trees in their native habitats (Gibson, 1992; Nitta and Ohsawa, 1997; White and Thien, 1985) where light levels (PPF) of less than full sun are expected. In our study, optimal rates of photosynthesis occurred in 45% PPF, with significant decreases occurring for most taxa when grown at 100% PPF. Photoinhibitory responses, varying in severity, were documented for all taxa, suggesting optimal growth in container-nursery production should occur in light levels below 100% PPF. Most nurseries propagate *Illiciums* by stem cuttings, or rarely by seed (Olsen and Ruter, 2001). Although several cultivars of *I. floridanum* and *parviflorum* are in the nursery trade (Dirr, 1998), *I. henryi* is most likely represented by a single clone from its original introduction into the United States. *Illicium henryi* was introduced by Woodlanders, Inc., Aiken S.C., as cuttings from a specimen growing at The Sir Harold Hillier Gardens and Arboretum, Romsey, Hampshire, U.K. (Bob McCartney, personal communication.). *Illicium lanceolatum* was introduced by Camellia Forest Nursery, Chapel Hill, N.C. as plants grown from seed from the Hangzhou Botanic Garden, Hangzhou, China in 1985 (Clifford Parks, personal communication). The clone of *I. lanceolatum* in our study, although perhaps not representing the species as a whole, outperformed the taxonomically and morphologically similar *I. henryi* in sun and shade, and may be a substitute for the more popularly grown *I. henryi*.

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