

Leaf optical properties as affected by shade in saplings of six tropical tree species differing in successional status

Rogéria Pereira Souza and Ivany F. M. Válio*

Departamento de Fisiologia Vegetal, Instituto de Biologia, Universidade Estadual de Campinas, CP 6109, CEP 13083-970, Campinas, SP, Brasil; *Corresponding author: ivalio@bol.com.br

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Tree species differing in successional status may present different responses to shade. Adjustments at leaf level may affect their optical properties, leading to changes in PAR (photosynthetically active radiation) absorbance. The aim of this study was to evaluate leaf optical properties as affected by understory shade in saplings of six tropical tree species differing in successional status and degree of shade tolerance. Chlorophyll content and specific leaf area (SLA) were also evaluated. The effects of shade on leaf optical properties and chlorophyll content differed among the studied species, whereas increased SLA was a common response for all species, reflecting the occurrence of thinner leaves under shade. The three studied shade-tolerant species - *Esenbeckia leiocarpa*, *Myroxylon peruiferum* and *Hymenaea courbaril* - presented a greater PAR absorbance under shade. The response of the shade-intolerant species was varied. While *Schizolobium parahyba* also showed a greater PAR absorbance under shade, *Chorisia speciosa* did not alter its spectral properties and *Cecropia pachystachya* presented an opposite pattern, with smaller absorbance under shade. Increases in leaf chlorophyll content were significant in the shade-tolerant species, whereas they were absent or of small magnitude in the shade-intolerant ones. Although the shade-induced decrease of leaf reflectance was the only response that safely discriminated tolerant from intolerant species, the adjustments in leaf chlorophyll content and optical properties were more consistent for the tolerant species.

Key words: Chlorophyll, leaf absorbance, shade tolerance, specific leaf area, successional species.

Alterações das propriedades ópticas de folhas em resposta a sombreamento em plantas jovens de seis espécies arbóreas tropicais pertencentes a diferentes estádios de sucessão: Espécies arbóreas tropicais pertencentes a diferentes estádios de sucessão podem apresentar diferentes respostas ao sombreamento. Ajustes apresentados ao nível das folhas podem afetar as propriedades ópticas, levando a alterações na absorvância da radiação fotossinteticamente ativa (RAF). O objetivo deste trabalho foi avaliar alterações das propriedades ópticas foliares em resposta ao sombreamento natural em plantas jovens de seis espécies arbóreas tropicais pertencentes a diferentes estádios de sucessão e com diferente grau de tolerância à sombra. Conteúdo de clorofila e área foliar específica (AFE) também foram avaliados. Os efeitos do sombreamento sobre as propriedades ópticas foliares e conteúdo de clorofila diferiram entre as espécies estudadas, ao passo que o aumento da AFE foi uma resposta comum, refletindo a ocorrência de folhas mais finas. As três espécies tolerantes à sombra - *Esenbeckia leiocarpa*, *Myroxylon peruiferum* e *Hymenaea courbaril* - apresentaram uma maior absorvância da RAF sob sombreamento. A resposta das espécies intolerantes à sombra foi variada. Enquanto *Schizolobium parahyba* também apresentou maior absorvância da RAF sob sombreamento, *Chorisia speciosa* não alterou suas propriedades espectrais e *Cecropia pachystachya* apresentou um padrão oposto de resposta, com menor absorvância sob sombreamento. Aumentos no conteúdo de clorofila foram significativos nas espécies tolerantes à sombra, ao passo que estiveram ausentes ou foram de pequena magnitude nas intolerantes. Embora a redução da reflectância foliar sob sombreamento tenha sido a única resposta que discriminou seguramente as espécies tolerantes das intolerantes, os ajustes no conteúdo de clorofila e nas propriedades ópticas das folhas foram mais consistentes para as espécies tolerantes.

Palavras-chave: absorvância foliar, área foliar específica, clorofila, espécies sucessionais, tolerância à sombra.

Studies on sun/shade acclimation have, in the last decades, focused on growth and/or photosynthetic alterations presented by tree species differing in successional status. Generally, late-successional shade-tolerant species show only a limited response to shade compared with the greater adjustments of early-successional light-demanding species (Osunkoya et al., 1994; Chazdon et al., 1996; Lee et al., 1996; Souza, 1996; Strauss-Debenedetti and Bazzaz, 1996). At the leaf level, adjustments to shade may involve, among others, alterations in leaf thickness and chlorophyll content (Lei et al., 1996; Lei and Lechowicz, 1997; Evans and Poorter, 2001). These leaf characteristics are important in determining leaf optical properties (Vogelmann, 1993), a topic which has been relatively less investigated. Some studies revealed no marked differences in leaf optical properties between groups of sun and shade species (Lee and Graham, 1986; Knapp and Carter, 1998) or between exposed and shaded leaves of particular species (Langenheim et al., 1984; McKiernan and Baker, 1991; Cao, 2000). Other studies, however, have found that, in shade tolerant species, a greater adjustment of leaf characteristics is presented, which can lead to a higher absorbance of photosynthetically active radiation (PAR) under the light-limited conditions of understories (St-Jacques et al., 1991; Poorter et al., 1995). The objective of this study was to evaluate leaf optical properties as affected by shade in saplings of six tropical tree species differing in successional status and degree of shade tolerance.

The study was carried out with the early-successional species *Cecropia pachystachya* Trec., *Schizolobium parahyba* (Vell.) Blake, the intermediate species *Chorisia speciosa* St. Hil. and the late-successional *Esenbeckia leiocarpa* Engl., *Myroxylon peruiferum* L.F. and *Hymenaea courbaril* L. The first three species can be considered shade-intolerant, whereas the three latter are shade-tolerant, based on their survival behavior under deep shade (Souza and Válio, 2001). Species will be designated by the genus name throughout. Plants were grown from seeds germinated under controlled conditions (constant light, PAR 14 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Seedlings were transplanted into trays and kept in a greenhouse until establishment. Once established, the seedlings were transplanted into 3.5 dm³ polyethylene bags filled with forest soil and were submitted either to full sun (FS) or natural shade (NS) treatments under field conditions. The field experiments were carried

out at Santa Genebra Reserve, an 2.52 km² area of semideciduous tropical vegetation situated in Campinas, SP, Brazil (22°44'45"S, 47°06'33"W, 670 m altitude). FS treatment consisted of exposing plants to full sun radiation in an open area adjacent to the forest, whereas in the NS treatment, plants were kept inside the forest under the shade imposed by the closed canopy. Irradiance under the shade treatment was 0.4 % to 2.4 % of full sun. Red/far-red ratio was 0.23 to 0.74 within the forest and 1.22 to 1.44 outside. Both measurements were carried out with a LI-1800 portable spectroradiometer (LI-COR). In the FS treatment, the bags were kept inside ditches in soil to avoid excessive heating of the root system. FS plants were watered daily and NS plants were watered when necessary. After approximately 100 d, plants were evaluated for leaf optical properties, chlorophyll content and specific leaf area (SLA).

Leaf reflectance and transmittance were recorded with a LI-1800-12S integrating sphere linked through a fiber optic cable to a LI-1800 portable spectroradiometer (LI-COR) at 400-750 nm in 2 nm intervals. Leaf absorbance was calculated as 1 - reflectance - transmittance. The measurements were performed for three leaves (two for *Esenbeckia*) from different plants of each species. Leaf chlorophyll content was measured from 80% acetone extracts according to Arnon (1949) and calculated on an area basis. Duplicated samplings from four plants per treatment were used. SLA was calculated as the ratio area/dry mass for five (*Myroxylon*), seven (*Schizolobium*) or ten (all other species) leaves of plants grown under each treatment. Data were analyzed through the Student t test or, in cases where it was not applicable, by the Wilcoxon test, both at 5 % level of probability.

The effects of understory shade on leaf optical properties and chlorophyll content differed among species, whereas increased SLA was a common response, despite being comparatively less accentuated in the three shade tolerant species, i.e., *Esenbeckia*, *Myroxylon* and *Hymenaea* (table 1). Increased SLA reflects the occurrence of thinner leaves, which are less costly to produce (Lee and Graham, 1986), being a frequent response observed to shade (Cao, 2000; Lee et al., 2000; Evans and Poorter, 2001). Increases in chlorophyll content (mass basis) are also an adaptive and common response to shade, since they can provide a higher light harvesting capacity in low-light environments (Lei et al., 1996; Lei and Lechowicz, 1997).

Nonetheless, chlorophyll content on an area basis – although also reported in some studies (Lei and Lechowicz, 1997; Lee et al., 2000) - can even be lower in shaded than in sunlit leaves due to the occurrence of thinner leaves in the former condition (Lee et al., 1990; Tinoco-Ojanguren and Pearcy, 1995). Here, despite the reduced leaf thickness under shade, a significantly higher total chlorophyll content (area basis) was found in four species - *Chorisia*, *Esenbeckia*, *Myroxylon* and *Hymenaea* (table 1). The increase in chlorophyll content was very marked for the latter three shade-tolerant species, whereas it was of a very small magnitude in *Chorisia*. For *Cecropia* and *Schizolobium*,

total chlorophyll content was similar under both growth conditions (table 1). Except for *Schizolobium*, all other species also presented decreases in the chlorophyll a/b ratio under shade, as observed for a number of species in other studies (Cao, 2000; Lee et al., 2000; Rosevear et al., 2001). Examples of no modifications or even increases in this ratio have also been reported, showing that, although common, the reduction in chlorophyll a/b is not an universal response (Murchie and Horton, 1997). The decreases in chlorophyll a/b ratio reflect a greater thylakoid stacking, which is likely to lead to a somewhat greater efficiency of light utilization under light-limited conditions (Anderson et al., 1988).

Table 1. Specific leaf area (SLA), chlorophyll content and chlorophyll a/b ratio of plants of *Cecropia pachystachya*, *Schizolobium parahyba*, *Chorisia speciosa*, *Esenbeckia leiocarpa*, *Myroxylon peruiferum* and *Hymenaea courbaril* grown under full sun (FS) and natural shade (NS) treatments. Values, within a species, followed by the same letter are not significantly different at $p \leq 0.05$.

Species	Treatment	SLA (dm ² .g ⁻¹)	Chlorophyll content (mg.cm ⁻²)			Chlorophyll a/b ratio
			Chlorophyll a	chlorophyll b	total	
<i>Cecropia pachystachya</i>	FS	1.70 b	0.029 a	0.011 a	0.039 a	2.65 a
	NS	4.43 a	0.025 b	0.011 a	0.036 a	2.37 b
<i>Schizolobium parahyba</i>	FS	2.23 b	0.028 a	0.021 a	0.049 a	1.35 b
	NS	5.61 a	0.032 a	0.013 b	0.046 a	2.42 a
<i>Chorisia speciosa</i>	FS	2.31 b	0.020 a	0.007 b	0.027 b	2.80 a
	NS	4.94 a	0.021 a	0.008 a	0.030 a	2.50 b
<i>Esenbeckia leiocarpa</i>	FS	1.86 b	0.022 b	0.008 b	0.030 b	2.69 a
	NS	3.47 a	0.042 a	0.017 a	0.059 a	2.44 b
<i>Myroxylon peruiferum</i>	FS	0.71 b	0.027 b	0.010 b	0.036 b	2.76 a
	NS	0.86 a	0.031 a	0.013 a	0.043 a	2.44 b
<i>Hymenaea courbaril</i>	FS	1.57 b	0.026 b	0.012 b	0.038 b	2.22 a
	NS	1.81 a	0.051 a	0.026 a	0.080 a	1.56 b

The three shade-tolerant species *Esenbeckia*, *Myroxylon* and *Hymenaea* and the shade-intolerant *Schizolobium* presented a significant greater PAR absorbance under shade, mainly in the range 500-700 nm (figure 1). This was achieved through reductions either in leaf transmittance (e.g. *Schizolobium*), in leaf reflectance (e.g. *Esenbeckia* and *Myroxylon*) or in both (e.g. *Hymenaea*) (table 2). In the latter three shade-tolerant species, the greater absorbance values may be, at least partially, explained by their increased chlorophyll content associated with their comparatively smaller reduction of

leaf thickness, the latter being a characteristic which is expected to bring an increase in leaf transmittance (Osborne and Raven, 1986; Tanner and Eller, 1986). Probably, in these species, the increase in the chlorophyll content was sufficient to more than offset the reduction in leaf thickness and the resulting tendency of higher transmittance. The occurrence of consistent relationships between PAR absorbance or reflectance and chlorophyll concentration (area basis) has been demonstrated elsewhere (Syvertsen et al., 1995; Evans and Poorter, 2001). However, the occurrence of other alterations in leaf structure, which

can contribute to maximize the effective pathlength of radiation within the leaf and thereby increase the probability of its absorption by photosynthetic pigments, can not be disregarded. Probably, this was the case for *Schizolobium*, whose increased leaf absorbance was not associated with an increased chlorophyll content. Accompanying the increases in PAR absorbance in these species, an absorbance increase in wavelengths a little beyond 700 nm was also registered, as demonstrated by the integrated values calculated for the range 700-750 nm (table 2). This fact was also noted in the study of St-Jacques et al. (1991). Lee and Graham (1986) presented data showing that plants can use quanta beyond 700 nm in photosynthesis. Considering the far-red enriched spectral quality of the shaded understory, the utilization of quanta in the range 700-750 nm may be an important response to increase the overall carbon gain of the plants (Lee and Graham, 1986).

The shade-intolerant species *Chorisia* practically did not alter the spectral properties of their leaves under shade (figure 1, table 2), although an increase in the chlorophyll content was observed (table 1). This increase, however, was of a small magnitude and probably not enough to provide a greater absorbance. In comparison with the other

species, the shade-intolerant *Cecropia* plants presented an opposite pattern of alteration in their leaf optical properties, with smaller absorbance and higher transmittance under shade (figure 1, table 2). This species did not show increases in chlorophyll content (table 1). Therefore, *Cecropia* plants seem to be unable to adjust their leaf anatomy and chlorophyll content in order to compensate the reduced leaf thickness and consequently increased transmittance under shade. This lack of response may be unfavorable for their maintenance in deeply shaded environments.

Owing to the response of *Schizolobium*, the shade-induced increases in leaf absorbance did not allow a clear discrimination between the studied shade-intolerant and -tolerant species, although they were a more consistent response in the latter group. On the other hand, the shade-induced decreases in leaf reflectance safely discriminated the two groups, being significant for the shade-tolerant species and absent in the shade-intolerant ones (table 2). Probably, this response was associated with the comparatively greater adjustments in the chlorophyll content presented by the tolerant species. These results may agree with St-Jacques et al. (1991) and Poorter et al. (1995),

Table 2. Integrated values of leaf absorbance, transmittance and reflectance of plants of *Cecropia pachystachya*, *Schizolobium parahyba*, *Chorisia speciosa*, *Esenbeckia leiocarpa*, *Myroxylon peruiferum* and *Hymenaea courbaril* grown under full sun (FS) and natural shade (NS) treatments. Values followed by the same letter are not significantly different at $p < 0.05$.

Species	Treatment	Integrated values (relative units)					
		400 - 750 nm waveband			700 - 750 nm waveband		
		Absorbance	Transmittance	Reflectance	Absorbance	Transmittance	Reflectance
<i>Cecropia pachystachya</i>	FS	275.08 a	32.97 b	41.92 a	15.12 a	15.96 b	18.92 a
	NS	255.77 b	47.03 a	47.15 a	13.41 b	18.65 a	17.93 a
<i>Schizolobium parahyba</i>	FS	261.11 b	30.50 a	58.36 a	13.34 b	15.69 a	20.97 a
	NS	287.36 a	23.52 b	39.09 a	15.98 a	14.23 a	19.78 a
<i>Chorisia speciosa</i>	FS	268.00 a	42.30 a	39.66 a	12.22 a	19.66 a	18.11 a
	NS	264.80 a	46.46 a	39.57 a	12.56 a	20.38 a	17.71 a
<i>Esenbeckia leiocarpa</i>	FS	259.60 b	35.43 a	54.93 a	9.65 b	18.00 a	22.35 a
	NS	287.96 a	30.60 a	37.44 b	17.42 a	16.13 a	17.09 b
<i>Myroxylon peruiferum</i>	FS	279.39 b	28.90 a	41.68 a	15.88 b	15.74 a	18.38 a
	NS	295.46 a	22.50 a	32.02 b	20.60 a	14.58 a	14.81 b
<i>Hymenaea courbaril</i>	FS	269.71 b	37.82 a	42.44 a	12.03 b	19.25 a	18.71 a
	NS	284.88 a	27.14 b	37.95 b	15.88 a	16.49 a	17.63 a

that suggested that a greater leaf plasticity is related to species shade tolerance. Accordingly, Lee et al. (2000) showed a great plasticity for leaf characters in a shade-tolerant species. So, whereas shade tolerant species usually show less extent of response to shade for several growth and photosynthetic

parameters, the reverse trend seems to occur in relation to the chlorophyll content and leaf optical properties, which may contribute to a greater capacity to maximize light harvesting under deep shade. Such capacity may be important for the successful exploitation of understory environments.

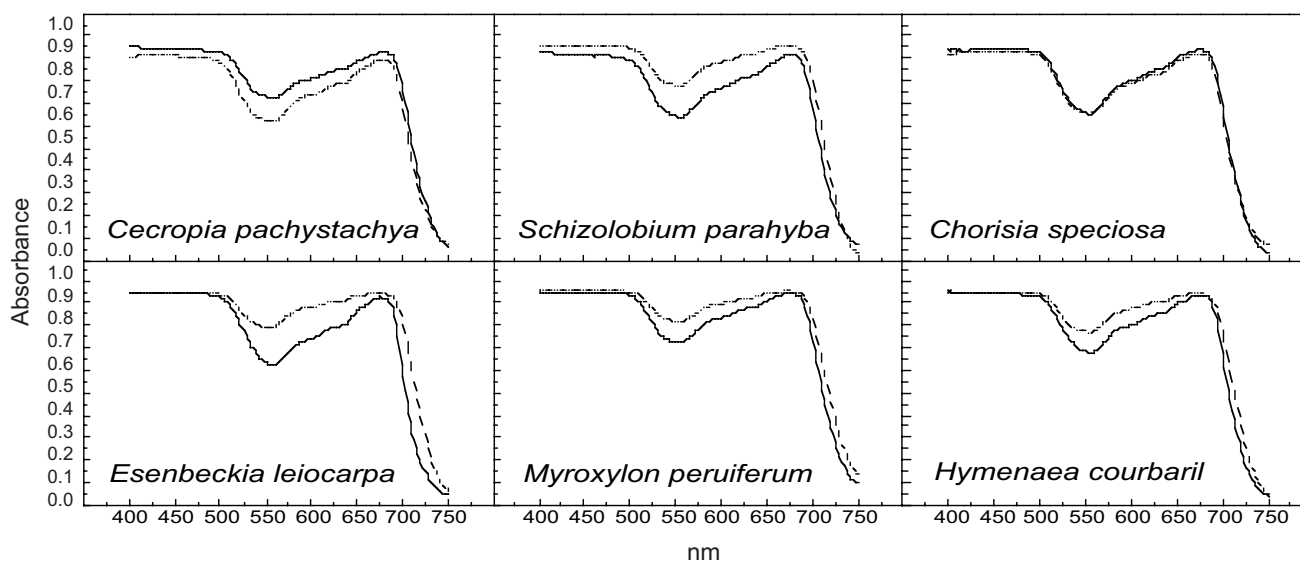


Figure 1. Leaf absorbance in *Cecropia pachystachya*, *Schizolobium parahyba*, *Chorisia speciosa*, *Esenbeckia leiocarpa*, *Myroxylon peruiferum* and *Hymenaea courbaril* plants grown under full sun (solid lines) and natural shade (dashed lines) treatments.

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