

Physiological Aspects of Sun and Shade Leaves of *Lithraea molleoides* (Vell.) Engl. (Anacardiaceae)

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ABSTRACT

The aim of this work was to compare the physiological parameters of sun and shade leaves of a specimen of *L. molleoides*. The higher-positional leaves, classified as sun leaves, presented similar photosynthetic rate, lower chlorophyll contents (a, b and total), same a chlorophyll /b chlorophyll rate, lower transpiratory rate, same stomatal conductance and intercellular concentration of CO₂ as the lower-positional leaves, classified as shade leaves. Nutrient concentration, except for Ca and Mg, was the same for both sun and shade leaves. The physiological parameter responses indicated that although receiving lower light intensity, the shade leaves had the same capacity to grow and develop as the sun leaves.

Key words: Photosynthesis, sun leaves, shade leaves, light intensity, chlorophyll, *Lithraea molleoides*

INTRODUCTION

In tropical forests, canopy opening, both by anthropic action and natural tree falling, or even canopy closing, produces a condition of light heterogeneity which is morphologically and physiologically reflected in the leaves (Chazdon and Fetcher, 1984; Kira and Yoda, 1989). Tree species are submitted to light variations as evidenced in the higher and lower portion of the same tree (Holbrook and Lund, 1995). Leaf response to different light conditions vary widely among species (Rijkers et al., 2000).

Overall, leaves growing under intense light display the following characteristics: higher mesophyll width, cuticle and photosynthetic rate

(Campostrini et al., 2001; Avalos and Mulkey, 1999; Oguchi et al., 2003). The highest photosynthetic rate in leaves exposed to intense light is associated to important morphoanatomic adaptations, especially greater cuticle and palisade parenchyma thickness, which allow the plant to minimize water loss and transmit the excess of light more directly, under more xeric conditions of the upper portion of the tree crown (Selleck and Shupert, 1957 apud Martinez and Medri, 1985) and to prevent photoinhibition (Lemos-Filho, 2000).

Lithraea molleoides (Vell.) Engl. (Anacardiaceae) is a native phanerogamous species, popularly known as aroeira (aroeira-branca, aroeira-brava, aroeira-do-brejo, aroeirinha, to name a few), 6 to

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12m tall, with a round-like crown. The leaves are composed of altern, imparipinnate, alado-petiolate (Barroso, 1984), 3-11 folioles, 5-8 cm long x 1.5-2.5 cm wide (Lorenzi, 2002). This species occurs in Minas Gerais, São Paulo, Mato Grosso do Sul down to Rio Grande do Sul, under many plant formations. It presents perennefolia, heliophyte and pioneer characteristics and is commonly found in forests located in altitude regions, both in dry and humid terrains.

L. molleoides is found in various types of environment, its investigation being thereby important not only to understand the distinct stages of a tropical forest dynamics but also to certify this species for reforestation of degraded areas. The plants are classified as sun plants and shade plants, depending on their capacity to adjust to differentiated light levels (Boardman, 1977). Such adaptation is directly related to the genotype of each species (Boardman, 1977; Rijkers, 2000). However, crown structure provides distinct environmental conditions to the leaves (Holbrook and Lund, 1995) and differentiated morphoanatomical and physiological characteristics can be noted in leaves developed in the high and low leaves of a same tree (Dale, 1992; Raven et al., 2001).

The objective of this work was to identify the adaptative strategies of a specimen of *L. molleoides* under light differences by attempting to find answers to the following questions:

- Is there a difference between the photosynthetic rate of leaves of *L. molleoides* developed under sunlight and under shade?
- Are there differences in chlorophyll content of a, b, and total chlorophyll between the leaves of *L. molleoides* developed in the sunlight and in the shade?
- Are there differences in transpiratory rate, stomatal conductance and intercellular concentration of CO₂ between *L. molleoides* leaves developed in the sunlight and in the shade?
- Is there a difference in nutrient concentration between the *L. molleoides* leaves developed under the sun and in the shade?

MATERIAL AND METHODS

This study was carried out in a specimen of *L. molleoides* localized at Ecological Klabin Park, Monte Alegre Farm in Telêmaco Borba - PR - 250

km from Curitiba-PR, second paranaense highland, mid east region (Fig. 1). The ecological park lies in a vegetational area dominated by Mixed Ombrophila Forest. In particular sites, vegetation is exuberant and composed by species typical of the more advanced successional stages, displaying a floristic richness, probably due to the ecotone zone (Nakajima et al., 1996).

For the physiological studies, ten sun leaves and ten shade leaves were collected from a *L. moleoides* plant. The sun leaves were collected from the peripheral upper portion of the plant and the shade plants from the internal lower portion. In order to determine the photosynthetic rate, stomatal conductance, transpiratory rate and CO₂, intercellular concentration were determined on the third foliole on the right, measured from the tip of the leaf toward the base. A portable infrared gas analyzer (A portable gas exchange system (Li-6400 (Li-Cor, Lincoln, NE, USA) was used for the evaluations. Light intensity used to evaluate the photosynthetic rate, stomatal conductance, transpiration, and CO₂ intercellular concentration was of 1.200 μmol m⁻² s⁻¹ selected after elaboration of a saturation curve.

Chlorophyll was quantified in the same leaves used to evaluate the parameters above described. The leaves were washed in deionized water, enclosed in black bags previously labeled and transported in ice from the field to the Embrapa-Soybean Ecophysiology Laboratory in Londrina-PR. Extraction and determination of chlorophyll contents followed the methodology by Arnon (1949), which consist of 80% acetone extracted, in the dark; the extracts obtained were centrifuged at a rotation of 2500 rpm over 10 minutes and the supernatants placed in 25 ml assay tubes wrapped in aluminum foil, with the volume being completed. The optical density of the substance was measured using a spectrophotometer at 645 and 663 nm. Based on the measurements, chlorophyll concentrations in the solutions were determined by using the formulas below, recommended by Arnon (1949):

$$\begin{aligned} \text{Total Chlorophyll (mg cm}^{-2}\text{)} &= \\ &[(A_{645} \cdot 20.2) + (A_{663} \cdot 8.02)] \cdot 0.025 / \text{area (cm}^2\text{)} \\ \text{a Chlorophyll (mg cm}^{-2}\text{)} &= \\ &[(12.7 \cdot A_{663} - 2.7 \cdot A_{645}) \cdot 0.025] / \text{area (cm}^2\text{)} \\ \text{b Chlorophyll (mg cm}^{-2}\text{)} &= \\ &[(22.9 \cdot A_{645} - 4.7 \cdot A_{663}) \cdot 0.025] / \text{area (cm}^2\text{)}. \end{aligned}$$

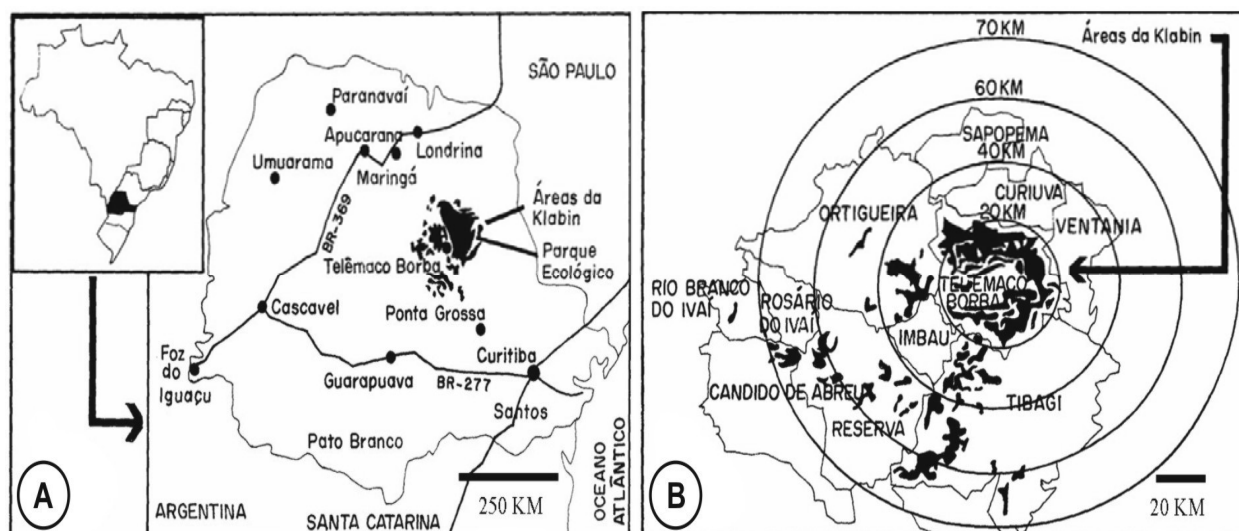


Figure 1 - Location of the Ecological Klabin Park, on Monte Alegre Farm- Telêmaco Borba, PR, where the studied species is found (A). The municipalities comprising Klabin - PR, area are shown in black (B).

To determine the macronutrients (N, P, K, Ca and Mg) and micronutrients (Zn, Mn, Fe, Cu and B), the leaves were washed in deionized water, placed into an oven at 60°C for 72, according to the EMBRAPA-Soybean Mineral Analysis Laboratory Methodology. Except for N, the nutrients were quantified in the equipment ICP-AES, model Optima 3300 DV. Sample digestion, except for N, was obtained with nitric acid (6N) using 0.5g of each sample. For nitrogen analysis the equipment Kjeltex, model 1035 Analyser Foss Tecator was used and sample digestion was obtained with sulphuric acid (PA) and hydrogen peroxyde, using 0.1g of each sample. Statistical analyses were conducted using Excel program, based on ANOVA (analysis of variance) at a 5% significance level.

RESULTS AND DISCUSSION

The photosynthetic rate of the sun leaves of *L. molleoides* was the same as that of the shade leaves (Fig. 2A). The contents of a, b, and total chlorophyll were higher in the shade leaves (Fig. 2B); a chlorophyll / b chlorophyll ratio did not differ in the leaves developed under the sunlight and shade of *L. molleoides* (Fig. 2C).

The transpiratory rate of the *L. molleoides* sun leaves was lower than that of the shade leaves (Fig. 3A). However, stomatal conductance (Fig. 3B) and CO₂ intercellular concentration (Fig. 3C) did not differ between leaves developed under sunlight and shade. Sun leaves showed a lower amount of nutrients, except for Ca and Mg which were the same, compared to the shade leaves (Table 1). The non-variation between the photosynthetic rate of sun leaves and shade leaves associated to higher chlorophyll contents in the shade leaves, likely due to a higher amount of photosystems in the membranes of the thylakoid of these leaves (Lemos-Filho, 2000; Damascos et al., 2006), indicated that shade leaves made an efficient use of the less intense irradiation reaching them. Besides the light effect on the photosynthetic process itself, synthesis and degradation of chlorophylls were also directly associated to light intensity (Engel and Poggiani, 1991). Avalos and Mulkey (1999) studying leaves of *Stigmaphyllon lindenianum*, Oguchi et al. (2003), leaves of *Chenopodium album* and Paiva et al. (2003), leaves of *Tradescantia pallida*, observed considerable changes in response to light differences, both in leaf structure and photosynthetic rate, which increased under greater light conditions.

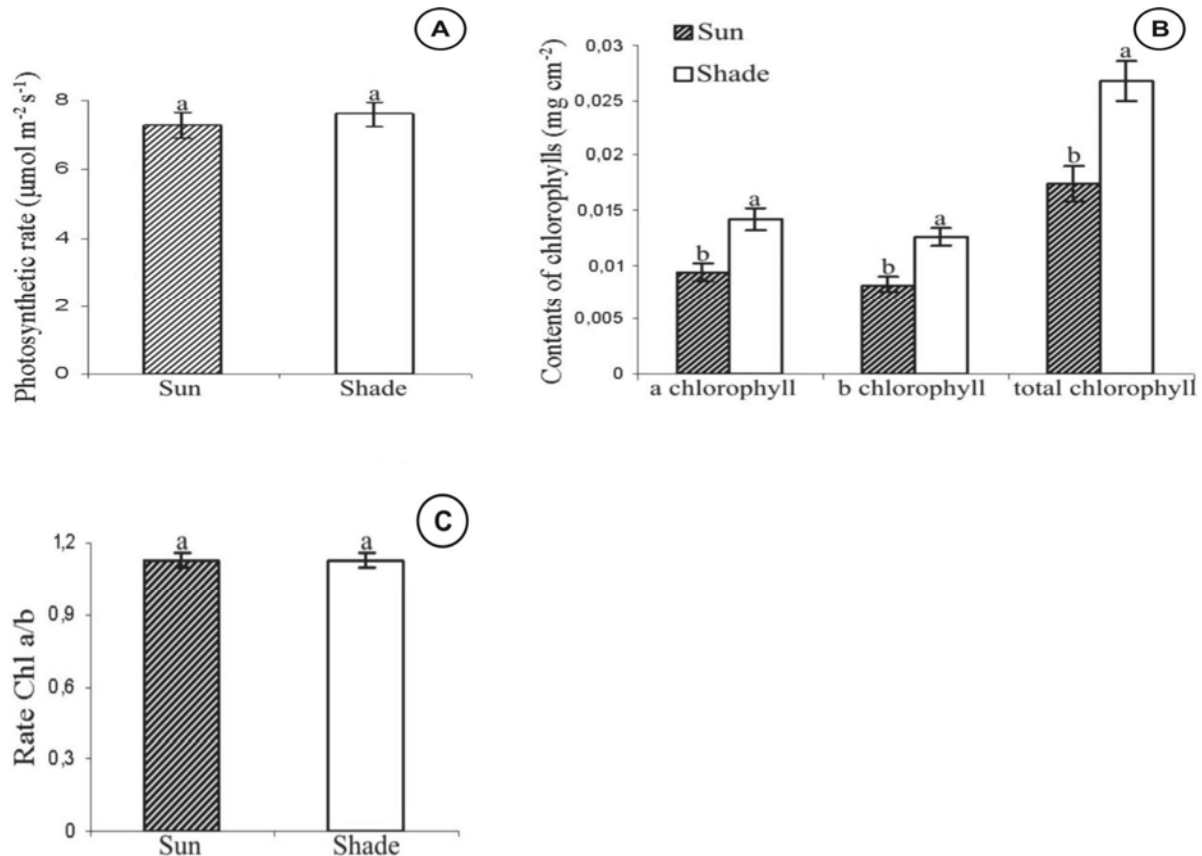


Figure 2 - Photosynthetic rate of *Lithraea molleoides* leaves developed under sunlight and shade (A). Same letters above the bars did not differ by the F test ($p \leq 0.05$, CV 15.45%). Contents of a, b, and total chlorophyll of *Lithraea molleoides* leaves developed under sunlight and shade (B). Different letters above each pair of bars differed by the F test ($p \leq 0.05$, CV 24.47% for a chlorophyll, CV 24.24% for b chlorophyll and CV 24.13% for total chlorophyll); a chlorophyll / b chlorophyll ratio (a/b Chl Ratio) of *Lithraea molleoides* leaves developed under sunlight and shade (C). Same letters above the bars did not differ by the F test ($p \leq 0.05$, CV 8.13%) ($n=10$). The vertical line on the upper part of the bars is the standard error.

Significant leaf structural changes were also identified in *L. molleoides* (Dias, 2005), but no photosynthetic rate increase was observed in leaves receiving more light. The higher level of chlorophyll in the shade leaves combined with structural change, such as greater intercellular space area of the spongy parenchyma, could be related with the non-differentiation of the photosynthetic rate between sun and shade leaves of *L. molleoides* (Dias, 2005). Higher chlorophyll contents in shade leaves were also observed by Souza and Valio (2003), studying the changes in leaf optical properties in response to shading on young plants of six tropical tree species of three different successional stages. Such chlorophyll

content increase was significant for the determination of tolerant species under shade. Although many studies observed higher chlorophyll contents in shaded leaves than in leaves exposed to greater light (Johnson et al., 1982; Sarracino et al., 1992; Chartzoulakis et al., 1995; Lei and Lechowicz, 1998), some authors did not find any difference among these proportions (Inoue, 1983; Graça, 1983; Kappel and Flore, 1983).

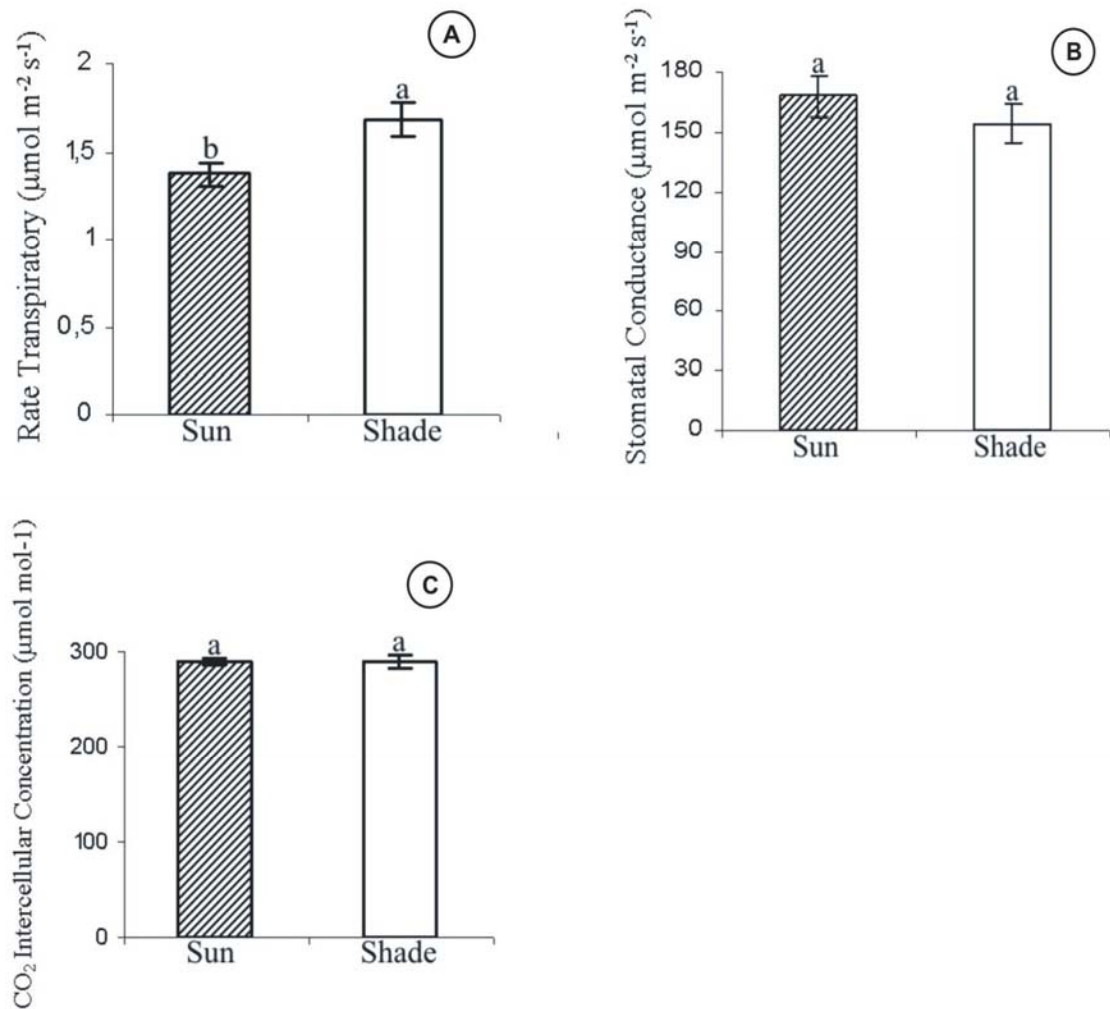


Figure 3 - Transpiration rate of *Lithraea molleoides* leaves developed under sunlight and shade (A). (CV 16.73%). Stomatal conductance of *Lithraea molleoides* leaves developed under sunlight and shade (B). (CV 19.87%). CO₂ intercellular concentration and *Lithraea molleoides* leaves developed under sunlight and shade (C). (CV 6.32%) (n=10). Same letters above the bars did not differ by the F test ($p \leq 0.05$). The vertical line on the upper part of the bars is the standard error.

Goryshina (1980), Engel and Poggiani (1991) and Atroch et al. (2001) also stressed a higher amount of chlorophyll by chloroplasts in leaves of lowland tropical forest tree species. In addition, several authors reported a higher a chlorophyll/b chlorophyll ratio in sun leaves (Johnson et al., 1982; Chartzoulakis et al., 1995; Lei and Lechowicz, 1998; Souza and Válio, 2003), than in leaves of *L. molleoides*.

Unaltered a chlorophyll /b chlorophyll ratio in *L. molleoides* was likely due to the fact that this species was a pioneer generally absent in closed places in the forests, since in these places it the

occurrence of species displaying leaves with a higher b chlorophyll amount was common to compensate a higher chlorophyll efficiency in absorbing the red wave length reaching the lowland (sub-bosque) (Kozłowski et al., 1991; Atroch et al., 2001; Taiz and Zeiger, 2004). Such adaptation occurs to maintain photosynthesis photochemical phase efficiency (Taiz and Zeiger, 2004).

The *L. molleoides* leaves developed under shade had a higher transpiratory rate than the leaves developed under sunlight. This fact was not observed by Morais et al. (2003) in study on the

physiological and growth traits of coffee plants shaded with guandu and cultivated under full sun. This study showed a decrease in leaf transpiration of the shaded coffee plants, likely due to the fact that coffee plants developed under full sun did not

present morphoanatomic adaptations sufficiently expressive to transpire less than the leaves developed under shade, as observed in *L. molleoides*.

Table 1 - Concentration of nutrients in *Lithraea molleoides* leaves developed under sunlight and shade. Averages followed by same letter did not differ by the F test ($p \leq 0.05$, $n=10$). The values between parentheses correspond to the standard error.

Nutrients	Sun	Shade	CV
	g 100 g ⁻¹		%
N	1.94 (± 0.058)b	2.44 (± 0.220)a	23.19
P	0.09 (± 0.002)b	0.11 (± 0.002)a	6.84
K	0.47 (± 0.020)b	0.60 (± 0.020)a	11.85
Ca	0,99 (± 0.16)a	1.02 (± 0.175)a	38.79
Mg	0.22 (± 0.004)a	0.29 (± 0.079)a	5.30
	. $\mu\text{g g}^{-1}$		
Zn	9.92 (± 0.573)b	11.3 ($\pm 0,260$)a	13.26
Mn	87.5 (± 2.335)b	101.0 ($\pm 2,206$)a	7.62
Fe	62.3 (± 1.862)b	97.6 ($\pm 2,235$)a	8.13
Cu	4.7 (± 0.183)b	5.2 ($\pm 0,124$)a	9.88
B	21.7 (± 0.592)b	28.4 ($\pm 0,423$)a	6.49

Stomatal conductance and CO₂ intercellular concentration were the same in sun and shade leaves of *L. molleoides*. This showed that even receiving a higher light intensity, the sun leaves had important morphoanatomic adaptations, allowing the same stomatal conductance and CO₂ intercellular concentration of the shade plants, also in agreement with the unchanged photosynthetic rate between the two types of leaves

In *Mangifera indica*, Castro Neto (2003) observed a lower stomatal conductance in sun leaves in the beginning of the irrigation period (end of May to August), suggesting this to occur due to the end of the water deficit period, since under irrigation, stomatal conductance increase although remaining lower than in the water deficit period. Cruz et al. (2003) observed in the cravo lemmoon tree submitted to saline stress, a lower stomatal conductance, with increased salinity content. Sultana et al. (1999) emphasized that a lower leaf stomatal conductance obtained by the plants under saline stress was probably related to the water stress to which these plants were subjected, as the leaves exposed to higher light. A lower stomatal conductance lead to a reduced normal CO₂ flux

towards the carboxylation site as well as a reduced photosynthetic rate (Xu et al., 1994). *L. molleoides* sun leaves had lower macronutrient and micronutrient values than the shade leaves, except for macronutrients Ca and Mg, which did not differ. Since the shade leaves had higher chlorophyll contents than the sun leaves and possibly the same photosynthetic rate in spite of lower light, the results indicated the important role played by most of these nutrients in the photosynthesis process (Clark, 1981; Neves et al., 2004), as they were part of the main molecules involved in the transfer of electrons during the light reactions and also as a source of energy (Taiz and Zeiger, 2004).

Similar Ca levels of the sun and shade leaves were in agreement with the fact that no variations were observed in the stomatal conductance between these two types of leaves (Malavolta, 1997). Both N and Mg were part of the chlorophyll molecules; however, when sun and shade leaves of *L. molleoides*, were compared, only N levels were observed to vary according to the chlorophyll levels, indicating that because these molecules had only one Mg atom, such variation was not

sufficient to allow the detection of significant differences in the Mg levels contrarily to N, as each chlorophyll molecule has four atoms of this element (Majerowicz, 2004).

Leitão and Silva (2004), in a study on seasonal variation of macronutrients in *Ouratea spectabilis*, a cerrado tree species, observed high contents of nitrogen, phosphorus, potassium, calcium, magnesium and sulphur in the vegetative organs of this species. It was evident that such higher macronutrient contents varied according to the vegetative organs and seasonality, but it was possible to note the efficient use of nutrients by this species, reflecting phenological and distributional patterns, which guarantee its survival in cerrado environments. This showed that the species presented important macronutrient and micronutrient variations based on the environmental conditions.

Neves et al. (2004), in a study on the growth and visual symptoms of micronutrient deficiencies in the umbu tree, a drought adapted species, stressed the importance of the role these micronutrients played in the photosynthetic process. For instance, Fe participates in enzymatic activation and photosynthesis, playing an important role in the process of biological fixation of N; Mn also participates in the photosynthesis, acting on the photo chemical release of O₂ and Zn participates mainly in the synthesis of AIA and cellular division (Malavolta et al., 1997).

It was possible that these physiological adaptations associated with the morphoanatomical adaptations of *L. molleoides* allowed the sun leaves higher assimilation of CO₂ by moles of transpired water. Besides, the fact that the sun leaves had more chlorophylls and higher nutritional levels allowed them to achieve the same photosynthetic rate as the sun leaves, despite being exposed to lower light. Combined with the morphoanatomical results, the physiological responses of this species showed relative capacity of success of this specime during the first successional forest stages. Such informations are important for the development of projects aiming the recovery of degraded areas.

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RESUMO

O presente trabalho teve como objetivo avaliar de forma comparativa alguns parâmetros fisiológicos de folhas de sol e de sombra de um espécime de *L. molleoides*. Esta espécie é conhecida popularmente como aroeira-branca. As folhas da porção superior periférica, denominadas folhas de sol, apresentaram igual taxa fotossintética, menores teores de clorofilas (a, b e totais), mesma razão clorofila a/ clorofila b, menor taxa transpiratória, mesma condutância estomática e concentração intercelular de CO₂ em relação às folhas da porção inferior interna, denominadas folhas de sombra. A concentração de nutrientes, excetuando Ca e Mg, foi igual em folhas de sol e de sombra. As respostas dos parâmetros fisiológicos avaliados indicam que as folhas de sombra, apesar de receberem menor intensidade luminosa, têm possibilidade de crescer e se desenvolver com a mesma capacidade das folhas de sol.

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