Vol.46, n. 2 : pp. 243-252, March 2003
ISSN 1516-8913 Printed in Brazil

**BRAZILIAN ARCHIVES OF
BIOLOGY AND TECHNOLOGY**
AN INTERNATIONAL JOURNAL

Growth and Photosynthetic Capacity in Two Woody Species of Cerrado Vegetation Under Different Radiation Availability

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ABSTRACT

Seedlings of two woody species of cerrado vegetation, Copaifera langsdorffii *and* Eriotheca gracilipes, *were studied under three different radiation availability (100, 80 and 30% transmittance). Full solar radiation brought about more biomass, higher total leaf area, higher maximal photosynthesis per crown on area or on mass bases and higher photosynthetic capacity on area bases. Only the photosynthetic capacity values on leaf mass bases were higher in both species under low radiation availability (80 and 30% transmittance). The differences of accumulated biomass appeared more clearly after 4 months of sowing but the root/shoot dry biomass ratio and height were maintained constant for both species independently of the available radiation. Cultivated under full solar radiation both species will be able to cover more suitable the two processes during seedling's phase: growth and defense.*

Key words: Biomass allocation, cerrado, *Copaifera langsdorffii, Eriotheca gracilipes,* growth in shade, photosynthesis

INTRODUCTION

Growth, defense and reproduction are processes that should be limited for a larger efficiency in use of available resources by plants (Bloom et al., 1985; Bazzaz et al., 1987; Chapin et al., 1990). Thus, the patterns of biomass allocation reveal how one species respond to the limited available resources. Therefore, the patterns of resource allocation (carbon and nutrients) are important to adaptation and can determine the species distribution.

In seedlings and saplings, there are only two competitive processes: growth and defense. The carbon in young plants are used not only to harmonize supply and demands, but also to minimize the risks during the life cycle using the stored carbohydrates in favorable periods (Chapin, et al., 1990). The roots of plants of cerrado are important stock site of carbon (Rizzini and Heringer, 1962) suggesting that the carbohydrates are accumulated underground at low costs in a favorable time in order to use it during stressful periods.

In addition to soil drought (Franco et al., 1996), low nutrient availability (Goodland and Pollard, 1973) and fire (Coutinho, 1978), radiation shortage is an important stress factor for autonomous young woody species of cerrado vegetation. If the germination occurs in *campo*

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limpo or in *campo sujo* physiognomic types, the herbaceous plants (specially grasses) will intercept the direct solar radiation before it reaches the seedling's leaves. If the woody species are growing under cerrado *sensu stricto* physiognomic type, the shrubs and trees will attenuate the photosynthetic active radiation. On the other hand, under forest physiognomic type of cerrado (the *cerradão*), radiation resource is limited by dense tree canopies even when a woody species achieves the sapling stage (cf. Coutinho, 1978). Therefore, the young woody species of cerrado should be able to respond to the available radiation during growth, changing the leaf metabolism associated to the carbon budget as the respiration rate, light compensation point, and photosynthetic capacity.

We studied the leaf gas exchange and dry matter partitioning in two young woody species of cerrado in order to detect important changes in leaf carbon metabolism and biomass allocation under different radiation availability. We aimed to highlight some adaptations at the leaf (carbon metabolism) and at the plant body (carbon allocation) levels that ensure the young woody species of cerrado to overcome the shortage of radiation availability and to complete their life cycle.

MATERIALS AND METHODS

Seeds of *Copaifera langsdorffii* Desf. (Caesalpinaceae) and *Eriotheca gracilipes* (K. Schum) A. Robins (Bombacaceae) were collected from adult plants grown in cerrado reservoir located at Federal University of São Carlos (UFSCar), municipality of São Carlos, Brasil (21°58' and 22°00' S - 47°51' and 47°52' W), between September-October, 1997. Using the Koeppen climatic classification, this region is classified as Cwa, tropical with dry winter and hot and wet summer being characterized by annual medium temperature of 21.3°C and annual precipitation of 1520 mm (Tolentino, 1967).

The two species studied are common in the cerrado reservoir of UFSCar producing high amount of seeds yearly. Both species are widespread in cerrado vegetation occurring also in forest (Ratter et al., 1996; Mendonça et al., 1998; Lorenzi, 1998). The analysis of floristic composition carried out by Ratter and Dargie (1992) in 26 areas of cerrado showed that *Copaifera langsdorffii* and *Eriotheca gracilipes* were present in 50% at all studied sites. Ratter et al. (1996) studying 98 areas (including Amazonian savanna) found *Copaifera langsdorffii* and *Eriotheca gracilipes* growing in 50 and 32%, respectively, in all sites studied.

The soil was collected on cerrado reservoir of UFSCar from an area of 6 m^2 and in depth of 20 cm. This soil was dried outdoor and stored in black plastic bags (10 kg capacity). The seeds of *C. langsdorffii* were first immersed in 98% sulfuric acid for three minutes in order to synchronize the germination (Prado et al., 1994) and the seeds of *E. gracilipes* were planted directly on soil.

The experiment was carried out in the experimental garden of Botany Department of UFSCar. The seedlings were maintained in greenhouse with 30 or 80% of transmittance with same air humidity and air temperature in relation to field conditions. In an open area, beside the greenhouses, a control parcel for both species under full solar radiation was installed (100% transmittance). During the whole experiment the soil was irrigated twice a week in all treatments until the field capacity. In each radiation condition 15 plants per species were maintained.

Three measurement at 120, 240 and 360 days after sowing (DAS) were realized for biomass determination between March and November 1998, using four individuals in each studied species at each time. The individuals were separated in root, shoot and leaves and dried at 60°C until constant weight.

Leaflets were collected in order to determine the specific leaf mass (SLM, g m^{-2}). Averages SLM values were obtained from three different individuals in both species studied. It was carried out drying 50 leaf discs (2-3 discs per leaflet) in *Copaifera langsdorffii* and 30 leaf discs (4-5 discs per leaflet) for *Eriotheca gracilipes* in each radiation treatment. SLM was calculated by dividing the mass of each disc per disc area according to Prado and Moraes (1997). The height of plants (cm) was determined using a millimeter ruler, from the root collar to the insertion of the last leaf. The total leaf area (cm^2) was determined by draw and weigh method.

The net photosynthesis rates were determined with a portable infrared gas analyzer (model LCA-4, ADC) connected to a narrow Parkinson Leaf

Chamber (PLCN-4, ADC). The artificial light during A-PPFD curves was provided by a light cannon (PLU-2, ADC) mounted on the head of the PLCN-4. The photosynthetic capacity (A_{max}) as a function of photosynthetic photon flux density (PPFD) was carried out in four month old plants, during the morning, between 7:00-9:00 h. The photosynthetic capacity values on mass bases (A_{maxm}) as a function of PPFD were obtained by dividing the photosynthetic capacity on area bases (A_{maxa}) per SLM mean value (Prado and Moraes, 1997). The leaflets investigated to determine the SLM and A_{max} were fully expanded and were free of predation or infection. Two leaflets from different leaves in three plants were measured previously and one of the six leaflets that showed the highest value of net photosynthesis was chosen to obtain the photosynthesis-radiance curve (A/PPFD). During photosynthesis measurements the leaflet temperature (24.1°C-26.3°C) and the chamber temperature (24.3°C-26.9°C) were controlled by a Peltier system manufactured by analytical development company (ADC, Hoddesdon, UK). The mean values of the maximal photosynthesis per crown on area (MPCA, μmol s^{-1}) and on mass bases (MPCM, μmol s^{-1}) were obtained by multiplying A_{maxa} (μmol m^{-2} s^{-1}) per total canopy leaf area (the average value, m^2) or by multiplying A_{maxm} (μmol kg s^{-1}) per total canopy leaf dry mass (the average value, kg), respectively, for each treatment. The equation used to adjust the values of A/PPFD curve was that utilized by Prado and Moraes (1997):

$$A= A_{max.}\,(1- e^{-k\,.(PPFD\ -\ LCP)}) \qquad (1)$$

where:
A= net photosynthesis
A_{max}= maximal net photosynthesis
e= logarithm on natural base
k= constant
PPFD= photosynthetic photon flux density
LCP= light compensation point

Radiation that saturated photosynthesis at 90% (LSP) and respiration in dark (Rd) were measured utilizing the equation (1) described above. Biomass, area and height data series were prior tested by Komogorov's test (Sokal and Rohlf, 1981) in order to verify their normal distribution. After that, these data were subjected to analysis of variance and the average values were tested by Tukey test (Vieira, 1991).

RESULTS AND DISCUSSION

Plants exposed to full solar radiation (100% of transmittance) presented the largest values of A_{maxa} (Fig.1). Some photoinibition occurred during A/PPFD curves in leaflets of *Eriotheca gracilipes* cultivated under 80% and 30% of transmittance since a slight decreasing rate of net photosynthesis above 1000 μmol m^{-2} s^{-1} was detected (Fig. 1). The higher carbon assimilation capacity by leaves growing under full solar radiation was expected due to their largest amount of enzymes related to carbon assimilation and higher capacity of electronic transport than shaded leaves (Björkman, 1981). The differences between A/PPFD curves on area and on mass bases in same species grown under same transmittance were only about the photosynthetic capacity values (A_{max}, Figs. 1 and 2).

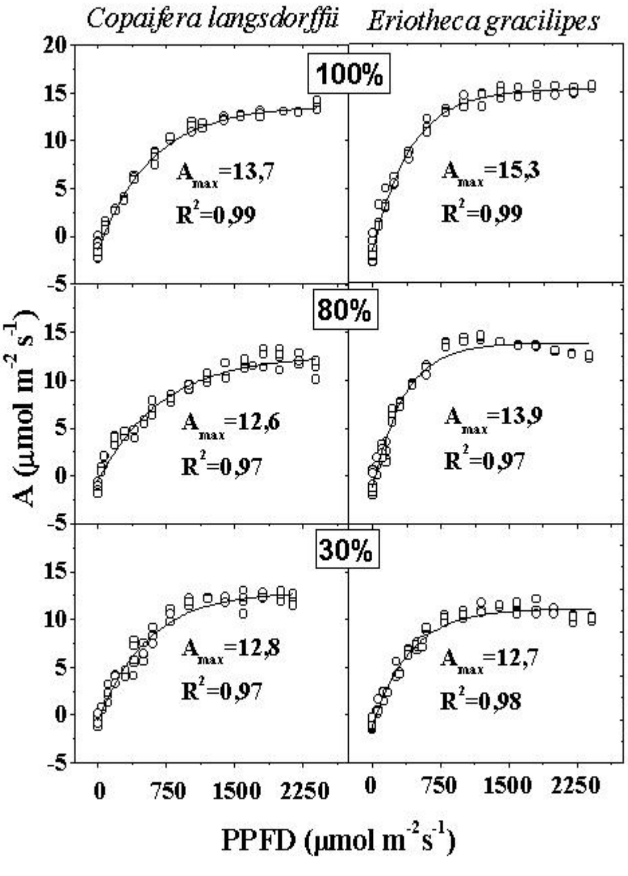

Figure 1 - Net photosynthesis. (A) expressed on area bases (A_{maxa}, μmol m^{-2} s^{-1}), as a function of photosynthetic photon flux density (PPFD) in totally expanded leaflets in *Copaifera langsdorffii* and in *Eriotheca gracilipes* at 120 days after sowing and cultivated at 100 (full solar radiation, top), 80 and 30% transmittance.

These values, when expressed on mass bases (A_{maxm}) showed an inverse tendency in relation to the results obtained for photosynthetic capacity on area bases (A_{maxa}). Hence, the values of A_{maxm} were larger in plants grown under lower radiance (Fig. 2). Therefore, using equation 1, the values of respiration in dark (R_d), light compensation point (LCP) and light saturation level (LSL) were identical in A/PPFD curves on area or on mass bases. Notwithstanding, higher values of LCP, LSL and R_d were obtained in seedlings that were grown under 100% of transmittance in both species (Table 1) besides their greater values of A_{maxa} (Figs. 1 and 2). Under lower transmittances (80 and 30%), *C. langsdorffii* and *E. gracilipes* altered their leaf carbon metabolism, reaching smaller values of LCP, LSL, R_d and A_{maxa}. Thus, lower values of A_{maxa} and R_d allowed some balance in regard to leaf carbon budget for both young species in shade. Generally, under lower transmittances, the formed leaf is simpler structurally (Larcher, 1995) showing a smaller amount of soluble proteins (Berry, 1975) and demanding smaller synthesis cost and cheaper maintenance due to its lower solicitation for respiration. Moreover, the maintenance of a positive carbon balance under low radiance is conditioned principally by respiration intensity, the main factor for shade tolerance (Medina, 1998).

However, this plasticity changing LCP, LSL, Rd, A_{maxa}, and A_{maxm} in both species studied was not enough to result in a more favorable carbon balance to the whole seedling cultivated in shade. Thus, both species under low irradiance had none effective result about the biomass accumulation in different plant compartments (Figs. 3 and 4) or in relation to the total leaf area (Tables 2 and 3).

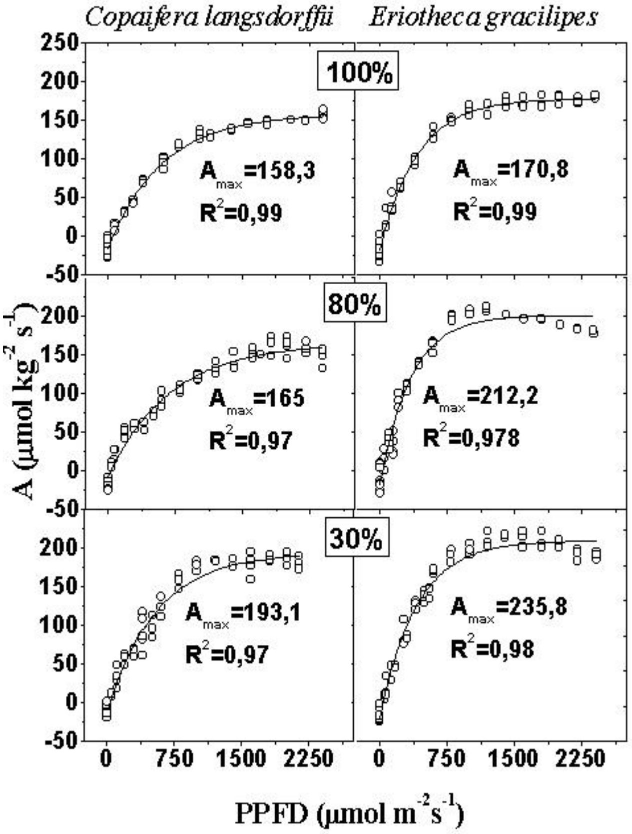

Figure 2 - Net photosynthesis (A) expressed on mass bases (A_{maxm}, μmol kg^{-1} s^{-1}), as a function of photosynthetic photon flux density (PPFD) in totally expanded leaflet in *Copaifera langsdorffii* and in *Eriotheca gracilipes* at 120 days after sowing and cultivated at 100 (full solar radiation, top), 80 and 30% transmittance.

Table 1 - Light compensation point (LCP, μmol CO_2, m^{-2} s^{-1}) light saturation level (LSL, μmol quanta m^{-2} s^{-1}) and respiration in dark (Rd, μmol CO_2 m^{-2} s^{-1}) of *Copaifera langsdorffii* and *Eriotheca gracilipes* at 120 days after sowing (DAS) cultivated under different radiation availability.

Species	Trans-mittance (%)	LCP μmol CO_2 m^{-2} s^{-1}	LSL μmol quanta m^{-2} s^{-1}	Rd μmol CO_2 m^{-2} s^{-1}
Copaifera langsdorffii	100	58	1400	1,4
	80	28	1195	0,5
	30	26	1296	0,6
Eriotheca gracilipes	100	41	1008	1,6
	80	28	819	1,2
	30	30	980	0,9

After 120 days, the seedlings of *C. langsdorffii* and *E. gracilipes* showed the largest values of root, shoot and total dry biomass when cultivated under full solar radiation (Figs. 3 and 4). Therefore, the lower root, shoot and total biomass in plants grown under low radiance were due to smaller amounts of resources (assimilated carbon) obtained for development under this condition. Such fact was not evidenced only by lower values of A_{maxa} on area basis (Fig. 1) but also by lower leaf area showed in both species cultivated at 30 and 80% of transmittance (Tables 2 and 3). In addition, the decreased development of the roots can be a consequence of faulty translocation of assimilated material from shoot to root in plants grown in shade (Lee et al., 1997).

Therefore, the results from Figs. 1 to 4 indicated that individuals in shade had less carbon for growth and probably for defense, the two vital processes during seedlings' phase. Hence, the greater result of A_{maxm} obtained in shade (Fig. 2) was just a consequence of some leaf physiological adaptation to decrease the leaf cost production as pointed out by Chapin et al., (1990).

The root/shoot ratio (Figs. 5 and 6) was favorable to root in all treatments, with exception to *C. langsdorffii* cultivated under 30% transmittance at 360 DAS (Figs. 5 and 6). Lower ratio of root/shoot on dry mass bases in shade condition seemed to be the predicted result because plants under low transmittances allocate relatively more carbon toward shoot in order to avoid the light deficit (Bloom et al., 1985). However, in this work this was not observed due to the typical characteristic of cerrado's species, which allocated more resources to roots (Rizzini and Heringer, 1962; Pogiani, 1971). In regard this, Chapin (1980) pointed out that plants of poor environment (*e.g.* unfertile soils of cerrado) showed lower plasticity concern the resource allocation pattern and the ratio root/shoot changes relatively little in response to environmental variation. Hence, the allocation storage process preferentially in roots was maintained by *C. langsdorffii* and *E. gracilipes* irrespective of the transmittance condition (Figs. 5 and 6).

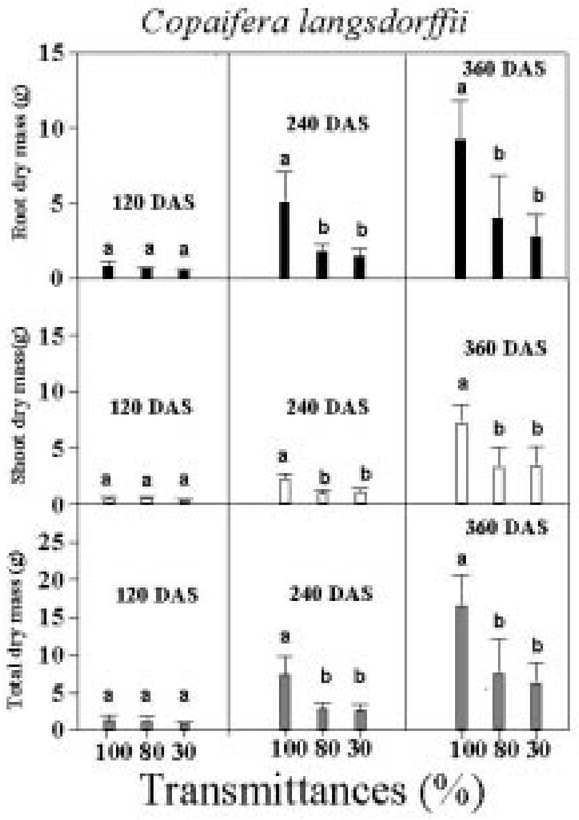

Figure 3 - Average (bars) and standard deviation (lines on the bars) values of root, shoot and total dry mass in *Copaifera langsdorffii* cultivated under 100, 80 and 30% transmittance at 120, 240 and 360 days after sowing (DAS). The same letters above the bars in same age (DAS) in different transmittances indicate that the average dry mass values do not differ statistically at $p<0.05$ by Tukey test.

The larger dry matter allocation to roots in plants of cerrado (building up a xylopodium) should be a carbohydrate storage purpose.

Stored carbohydrates are resources quickly available to vital process in young plants (growth and defense). The saved carbon in roots is protected against folivorous' attack or even against fire, a common event in cerrado vegetation (Coutinho, 1978). Usually, these carbohydrate material is accumulated in a favorable time in order to utilize it when acquisition is more difficult decreasing all costs involved (Chapin et al., 1990).

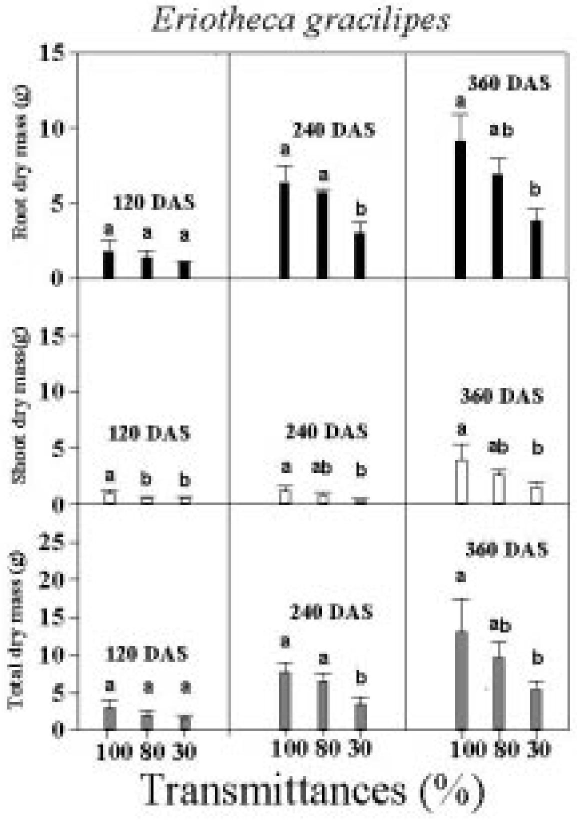

Figure 4 - Average (bars) and standard deviation (lines on the bars) values of root, shoot and total dry mass in *Eriotheca gracilipes* cultivated under 100, 80 and 30% transmittance at 120, 240 and 360 days after sowing (DAS). The same letters above the bars in same age (DAS) in different transmittances indicate that the average dry mass values do not differ statistically at p<0.05 by Tukey test.

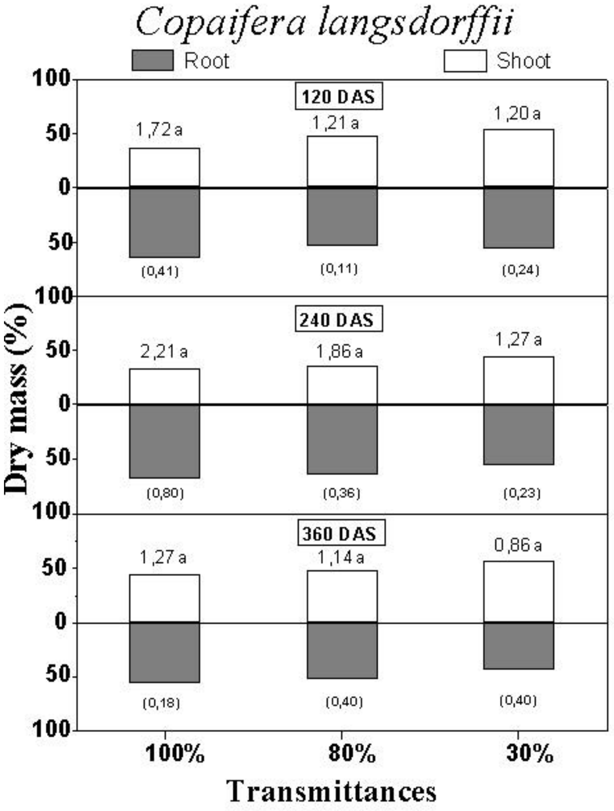

Figure 5 - Mean values of the root/shoot ratio (above the bars) in *Copaifera langsdorffii* at 120, 240 and 360 days after sowing (DAS) grown under different radiation availability (100, 80 and 30% of transmittance). The bars indicate the percentage of each plant part (root or shoot). Values between parenthesis are the standard deviation of the root/shoot ratio. Mean values followed by same letter in same age (DAS) are not significantly different in Tukey test (p<0.05).

SLM values were significantly higher in plants cultivated under 100% transmittance in both species at all determinations (Tables 2 and 3). The leaf area at 120 and 360 DAS did not differ significantly among the radiation treatments in *C. langsdorffii*. However, at 240 DAS the leaf area values were superior under full solar radiation. In *E. gracilipes* the leaf area value at 120 and 240 DAS were superior under 100% of transmittance but they did not differ at 360 DAS. The height was similar in both species at all ages and radiation condition.

The smaller leaf area in shade (Tables 2 and 3) occurred due to the lower carbon assimilation under this condition and, as a consequence, there was not enough amount of carbohydrates to produce and support a larger shoot development.

Under low transmittances the growth of a leaf continues until it reaches an area that maximizes the net photosynthesis. It happens because the increment in leaf area requests the development of new support structures and vascular tissues increasing the marginal costs to rise the production (Chapin et al., 1990). Under lower transmittance both species did not have enough amount of carbon to support these marginal costs. New leaf area production stops as soon as there is smaller return in relation to the corresponding investments (Bloom et al., 1985).

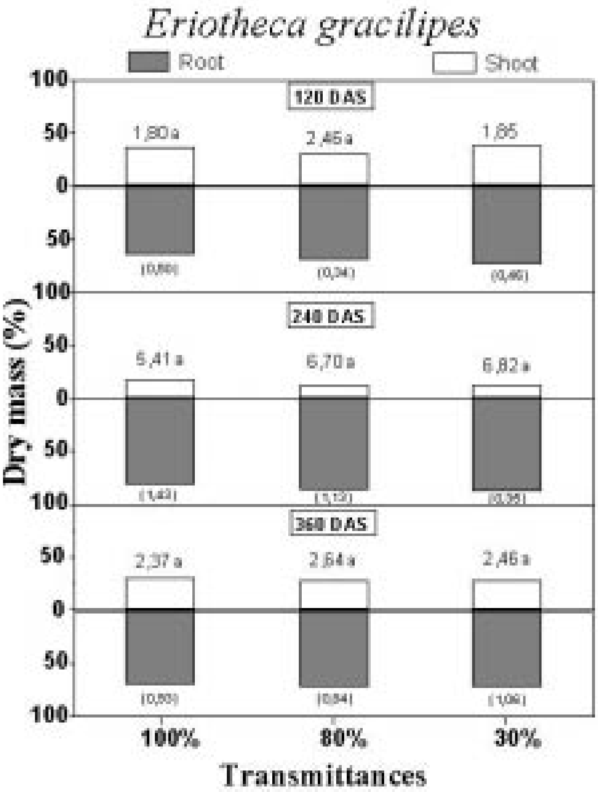

Figure 6 - Mean values of the root/shoot ratio (above the bars) in *Eriotheca gracilipes* at 120, 240 and 360 days after sowing (DAS) grown under different radiation availability (100, 80 and 30% of transmittance). The bars indicate the percentage of each plant part (root or shoot). Values between parenthesis are the standard deviation of the root/shoot ratio. Mean values followed by same letter in same age (DAS) are not significantly different in Tukey test ($p<0.05$).

The lower mean values of SLM reached by plants grown under low transmittance (Tables 1 and 2) indicated that they invested less in leaves structure. The leaves of both species probably adapt to the radiation stress decreasing its thickness, cellular layers number and increasing the intercellular spaces in shade (Larcher, 1995). By these morphological alterations the plant decreases the synthesis and the maintenance of leaf costs, increases relatively the CO_2 absorption and produces a leaf characteristically simpler, which required low demand of carbon and becoming easier to replace. The replacement cost of the lost tissue is relatively higher in shade and there is not saved carbon or the storage available for leaf replacement is scarce in such radiation condition (Coley et al., 1985). Therefore, it is reasonable to suppose that one characteristic of plants cultivated under low transmittance is more allocation resources for defense than for growth (Kitagima, 1994). Thus, for both species studied in an environment with low radiation intensity only a low growth rate can be supported and the total physiology of the seedling works in agreement with the available resource (Bloom et al., 1985).

Lower SLM values of *C. langsdorffii* and *E. gracilipes* cultivated under low transmittances (Tables 2 and 3) suggested some leaf plasticity in both species and helped to understand the highest values of maximal photosynthesis per crown on area (MPCA) and mass basis (MPCM) reached under higher transmittance (Tables 4 and 5).

Highest MPCA and MPCM values were obtained by both species cultivated under full solar radiation (100% of transmittance, Tables 4 and 5). These results presented an inverse tendency in relation to those obtained for photosynthetic capacity on mass basis (A_{maxm}, Fig. 1). It showed that values of A_{maxm} were just one adjustment to shade condition. Thus, some physiological and morphological fittings occurred in leaflets but they were not extended to other more complex structures (*e.g.* crown) providing an increase in assimilation capacity of the whole seedling. Thus, the highest values of A_{maxa}, MPCA and leaf area obtained in plants cultivated under full solar radiation (Tables 4 and 5) could explain the largest total biomass accumulation under 100% transmittance.

Table 2 - Mean values ± standard deviation of the specific leaf mass (SLM), plant height and leaf area of *Copaifera langsdorffii* at 120, 240 and 360 days after sowing (DAS) under different light treatments (100, 80 and 30% of transmittance). Average values in column for each parameter in same age (DAS) followed by same letters are not significantly different in Tukey test ($p<0.05$).

Transmittance (%)		**D A S**		
		120	240	360
SLM (g m^{-2})	100	86,7a	92,3a	93,8a
		± 6,7	± 6,7	± 7,9
	80	76,5b	82,1b	83,7b
		± 7,2	± 7,6	± 8,7
	30	66,3c	70,9c	71,9c
		± 8,6	± 8,1	± 8,2
Plant height (cm)	100	13,5a	19,3a	45,2a
		± 1,9	± 4,9	± 4,6
	80	12,6a	15,1a	35,2a
		± 2,2	± 0,5	± 2,9
	30	13,8a	15,8a	41,5a
		± 1,8	± 1,3	± 9,1
Leaf area (cm^2)	100	56,6a	176,2a	409,7a
		± 16,4	± 44,9	± 47,7
	80	56,3a	87,8b	316,9a
		± 12,8	± 17,7	± 120,2
	30	53,6a	103,1b	299,0a
		± 12,8	± 36,0	± 132,0

Table 3 - Mean values ± standard deviation of the specific leaf mass (SLM), plant height and leaf area of *Eriotheca gracilipes* at 120, 240 and 360 days after sowing (DAS) under different light treatments (100, 80 and 30% of transmittance). Average values in column for each parameter in same age (DAS) followed by same letters are not significantly different in Tukey test ($p<0.05$).

Transmittance (%)		**D A S**		
		120	240	360
SLM (g m^{-2})	100	86,0a	86,4a	89,2a
		± 11,8	± 7,9	± 10,3
	80	69,5b	70,7b	76,0b
		± 9,8	± 5,2	± 6,4
	30	53,9c	54,5c	57,5c
		± 5,8	± 5,7	± 8,9
Plant height (cm)	100	11,6a	14,3a	30,2a
		± 1,9	± 1,0	± 4,7
	80	9,7a	12,8a	27,2a
		± 1,6	± 0,7	± 2,5
	30	10,7a	12,1a	25,0a
		± 2,9	± 1,2	± 3,9
Leaf Area (cm^2)	100	95,4a	118,5a	302,0a
		± 19,1	± 27,3	± 68,9
	80	57,7b	114,7a	221,4a
		± 15,9	± 23,3	± 24,7
	30	84,0ab	75,5b	204,4a
		± 21,1	± 17,9	± 54,6

Table 4 - Maximum photosynthesis per crown on area bases (MPCA) and on mass bases (MPCM) in *Copaifera langsdorffii* at the 120, 240 and 360 days after sowing (DAS) cultivated under 100 (full solar radiation), 80 and 30% transmittance. Average values in column followed by same letter in same age (DAS) for each parameter do not differ significantly by Tukey test ($p<0.05$).

Transmittance (%)		**D A S**		
		120	240	360
MPCA (µmol s^{-1})	100	0,78 a	2,42 a	4,15 a
	80	0,71 a	1,11 b	2,80 b
	30	0,68 a	1,32 b	2,61 b
MPCM (µmol s^{-1})	100	0,06 a	0,15 a	0,59 a
	80	0,06 a	0,11 b	0,37ab
	30	0,05 a	0,11 b	0,33 b

Table 5 - Maximum photosynthesis per crown on area bases (MPCA) and on mass bases (MPCM) in *Eriotheca gracilipes* at the 120, 240 and 360 days after sowing (DAS) cultivated under 100 (full solar radiation), 80 and 30% transmittance. Average values in column followed by same letter in same age (DAS) for each parameter do not differ significantly by Tukey test ($p<0.05$).

Transmittance (%)		**D A S**		
		120	240	360
MPCA (µmol s^{-1})	100	1,46 a	1,82 a	6,27 a
	80	0,81 b	1,60 a	4,41 b
	30	1,07ab	0.96 b	3,80 b
MPCM (µmol s^{-1})	100	0,15 a	0,16 a	0,53 a
	80	0,10 a	0,14ab	0,38 b
	30	0,12 a	0,09 b	0,30 b

It could be concluded, that full solar radiation was an effective and positive resource for growth in both species studied, providing higher photosynthetic capacity at leaf and at crown levels, larger biomass accumulation in different compartments of the seedlings and larger total leaf area. Both species cultivated in shade (*e.g.* 30% transmittance) arduously could carry out sexual reproduction. At first sight, the studied species cultivated in shade would not have resources to sustain the demands from high-priced reproductive structures (Bazzaz et al. 1987). Notwithstanding, these species would probably tolerate the shade of 30% transmittance under field conditions, staying in vegetative stage with lower rates of growth.

RESUMO

Duas espécies de cerrado (*Copaifera langsdorffii e Eriotheca gracilipes*) foram cultivadas sob três diferentes condições de radiação (100, 80 e 30% de transmitância). A radiação solar plena proporcionou as condições mais favoráveis para o desenvolvimento das espécies: maior acúmulo de biomassa total, maior área foliar total, maior fotossíntese potencial por copa expressa em área ou em massa e maior capacidade fotossintética expressa em área foliar. Somente os valores de capacidade fotossintética expressa em massa foram maiores sob baixa radiação (80 e 30% de transmitância) para ambas as espécies. As diferenças de biomassa acumulada apareceram mais claramente após os 4 meses de plantio, mas a relação massa seca raiz/parte aérea e a altura foram mantidas independentes da radiação disponível para ambas as espécies. Sob 100% de transmitância estas espécies apresentaram um balanço de carbono mais positivo e condições mais favoráveis para suprir as duas principais demandas neste estágio do ciclo de vida da planta: o crescimento e a defesa.

ACKNOWLEDGEMENTS

We acknowledge “Conselho Nacional de Desenvolvimento Científico e Tecnológico” (CNPq, Pronex) and “Fundo Nacional do Meio Ambiente” (FNMA) for financial support.

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Received: April 18, 2001;
Revised: July 27, 2001;
Accepted: February 08, 2002.