

# PHYSIOLOGICAL RESPONSES OF *Vismia guianensis* TO CONTRASTING LIGHT ENVIRONMENTS<sup>1</sup>

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**ABSTRACT-** Changes in growth, biomass allocation patterns and CO<sub>2</sub> exchange were investigated in *Vismia guianensis* (Aubl.) Choisy, a medium tree known to invade forest gaps, active pastures and abandoned agricultural areas in Brazilian Amazonia. Plants were grown in controlled environment cabinets, under high (800-1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and low (120-200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) light regimes, during a 60-day period. No significant differences in CO<sub>2</sub> assimilation could be detected between high-light and low-light grown plants in the light response curve. However, dark respiration was higher on high-light grown plants. Relative growth rates were initially similar between light regimes, becoming higher for high-light at the subsequent harvests. Leaf area per unit dry mass of whole plant and leaf area per unit of leaf dry mass were higher for low-light grown plants. The proportion of biomass allocated to leaves was similar between treatments, while root matter per plant dry matter was 15 % higher for high-light and stem matter per plant dry matter was 13 % higher for low-light grown plants. These results suggest that the differential responses of this species to light conditions may contribute to or detract from its ability to succeed in natural and agricultural environments or to respond to weed control strategies.

**Additional index terms:** Biomass allocation patterns, growth analysis, photosynthesis, Amazonia.

## RESPOSTAS FISIOLÓGICAS DE *Vismia guianensis* A DIFERENTES CONDIÇÕES DE LUMINOSIDADE

**RESUMO-** Investigou-se por um período de 60 dias em câmara de crescimento, sob alto (800-1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) e baixo (120-200  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) regimes de luz os padrões de crescimento e distribuição de biomassa e as trocas gasosas de *Vismia guianensis* (Aubl.) Choisy, uma árvore de porte médio, comum como planta invasora de pastagens, áreas agrícolas abandonadas, e clareiras de floresta na Amazônia brasileira. Não foram detectadas diferenças em assimilação

de CO<sub>2</sub> na curva de resposta a luz entre plantas cultivadas sob alta e baixa radiação. No entanto, a respiração foi maior em plantas sob alta radiação. A taxa de crescimento relativo foi inicialmente similar entre regimes de luz, tomando-se maior para alta radiação nas avaliações subsequentes. A área foliar por unidade de massa total da planta e por unidade de massa da folha foram maiores para baixa radiação. A proporção de biomassa alocada para folhas foi semelhante entre tratamentos, enquanto a alocação de biomassa para as raízes foi maior em alta radiação e a alocação de biomassa para hastes e pecíolos foi maior em baixa radiação. Estes resultados sugerem que as respostas dessa espécie a variações nas condições de luminosidade são importantes para o seu sucesso em ambientes naturais e agrícolas ou a sua resposta a práticas de controle.

**Termos adicionais para indexação:** Alocação de biomassa, análise de crescimento, fotossíntese, Amazônia.

## INTRODUCTION

Depending on their acclimation capacity, plants can have distinct responses to the light environment (quantity and quality of light) (e.g., Clough et al., 1979; Givnish, 1988; Seemann, 1989; Walters & Field, 1987). The ability of a species to efficiently and rapidly adjust its allocation patterns and physiological behavior in response to a low or high light environment (holding quality constant) is key in determining its growth potential to that specific environment.

Knowledge of the morphological and physiological responses of invading species to contrasting light conditions can be critical in helping to explain and predict their occurrence and abundance patterns under specific environmental conditions. Moreover this information can be useful to explain the invasive potential and the competitive ability of these plants under different management in agricultural areas.

*Vismia guianensis* (Aubl.) Choisy (Guttiferae) is a native successional woody species from tropical America found as a colonizer of man-made clearings and natural gaps in forests and in abandoned or active agricultural areas in Brazilian Amazonia

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(Albuquerque, 1980; Dantas, 1989; Dias-Filho, 1990). In this paper it is investigated the sun-shade acclimation characteristics of *Vismia* by measuring its rate of growth, biomass allocation patterns, and photosynthetic features in response to high and low photon flux densities. The results are discussed in relation to their ecological and practical implications.

## MATERIAL AND METHODS

**Plant material and growing conditions-** *Vismia guianensis* (Aubl.) Choisy seeds were collected from plants growing in pasture areas near Paragominas, PA (3° 05' S - 47° 21' W) in Eastern Brazilian Amazonia. Seeds were germinated on filter paper in petri dishes and then planted individually in 150 mm plastic pots with a mixture of peat:vermiculite:perlite (1:1:1). Plants were initially grown in a greenhouse at temperatures of 24 ( 2.2 °C (minimum) to 33 ( 2.1 °C (maximum), and a maximum photosynthetic photon flux density (PPFD) of approximately 900  $\mu\text{mol m}^{-2} \text{s}^{-1}$ . When plants were about 25 days old they were transferred to a Conviron growth chamber (Model PGW36. Controlled Environments, Inc. Pembina, ND) set at 28/25 °C day/night air temperatures, 80 % relative humidity, and 12-h photoperiod. Before transference to the growth chamber, seedlings were divided into five size classes, and each class was randomly assigned to a replication (block).

A high- and a low-light environment were simulated by placing multiple layers of neutral density shade cloth beneath the light source of half of the growth chamber. Irradiance, monitored throughout the experiment with a quantum meter (Model LI-1905 light meter, Li-Cor, Inc. Lincoln, NE) at canopy height ranged between 800 and 1000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for high-light and between 120 and 200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for low-light treatment. During the first and the last hours of photoperiod, lights were set to a lower level to provide plants with a more gradual transition between light and dark. These transitional light levels measured at canopy height, ranged between 300 and 450  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for high-light and from 50 to 80  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for the low-light treatment.

All pots were watered daily to full capacity with deionized water and fertilized every other day with 50 ml per pot of a water soluble fertilizer solution (150 g  $\text{L}^{-1}$  N, 300 g  $\text{L}^{-1}$   $\text{P}_2\text{O}_5$ , 150 g  $\text{L}^{-1}$   $\text{K}_2\text{O}$ , 0.2 g  $\text{L}^{-1}$  B, 0.7 g  $\text{L}^{-1}$  Cu, 1.5 g  $\text{L}^{-1}$  Fe, 0.5 g  $\text{L}^{-1}$  Mn, 0.005 g  $\text{L}^{-1}$  Mo and 0.6 g  $\text{L}^{-1}$  Zn), (3.5mL  $\text{L}^{-1}$ ).

**Growth analysis-** Five harvests were made; the first harvest was on the day plants were transferred to the growth chamber (Day 0), and the others 15, 30, 45 and 60 days later (n=5 per harvest and light treatment). At each harvest plant material was divided into leaves, support tissues (stem and petiole) and roots. Leaves were removed and its area was measured using a leaf area meter (Model LI- 3000, Li-Cor, Inc. Lincoln, NE, with and conveyor belt assembly Model LI-3050, Li-Cor,

Inc. Lincoh, NE). Plant dry mass was obtained by drying the plant material in an oven at 70 °C for 48 hours. At each harvest the relative growth rate (change in dry matter per total dry matter of plant per day, RGR) and the following biomass allocation patterns were estimated according to Hunt (1990): leaf area ratio (leaf area per unit dry mass of whole plant, LAR), specific leaf area (leaf area per unit of leaf dry mass, SLA) and leaf, stem and root mass ratios (respectively, leaf, stem or root dry mass per unit of dry mass of whole plant, LMR, SMR and RMR).

**Gas exchange-** Gas exchange variables, calculated on a leaf area basis, were measured on plants just before the fifth harvest, i.e., after the plants had been in the growth chamber for 60 days. A photosynthesis (A) versus irradiance (PPFD) response curve (starting at ca. 1200  $\mu\text{mol m}^{-2} \text{s}^{-1}$  and decreasing in five steps to 0), was constructed in the laboratory on the most recent, fully expanded intact leaf of each plant using a portable photosynthesis system (Model LI-6200, LI-COR, Inc., Lincoln, NE). The amount of leaf area in the chamber (cuvette) was approximately 2.0  $10^{-3} \text{m}^2$ . Different irradiance levels were obtained by combining neutral-density filters between the leaf chamber and the light source, a high-pressure sodium vapor lamp (1000 W). Gas exchange measurements started after an adjustment period of about 20 min to each light level. To absorb long-wave radiation and maintain constant leaf temperatures in the cuvette, a 100 mm deep Plexiglas circulating bath of cool water was suspended between the light source and the leaf cuvette. After exposure to the lowest PPFD, the plants were left for 30 min in the dark for measurements of dark respiration ( $R_d$ ) values. Five replicate plants per treatment and one leaf per plant were sampled. The leaf-to-air vapor pressure gradient inside the cuvette during all measurements was 9-12 mmol  $\text{mol}^{-1}$ .

Gas exchange versus irradiance response data provided direct estimates of highest measured values of photosynthetic rate ( $A_{\text{max}}$ ). Apparent quantum yield of  $\text{CO}_2$  to incident irradiance ( $\alpha$ ) was calculated according to Thompson et al. (1992b): the slope of a regression of five  $R_d$  measurements and five low light (ca. 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) measurements of  $\text{CO}_2$  exchange, for each light regime combination. The light compensation point was calculated as the ratio,  $R_d/\alpha$ .

**Experimental design and statistical analysis-** The experiment was arranged in a randomized complete block design with five replications. All pots were rotated within replications (blocks) every day to minimize variation in growth due to possible temperature and light differences within the growth chamber.

Analysis of variance (ANOVA) was used to estimate the overall effects of light regime and harvest date and their interaction on biomass allocation parameters. The assumption of homogeneity of variances and normality was tested

for each ANOVA and when necessary data was logarithmically transformed. Transformed values were retransformed for presentation. Differences in RGR were tested as a Light regime x Time interaction in an ANOVA with logarithmically-transformed dry matter as dependent variable (Poorter & Lewis, 1986). A trend analysis over time was performed to detect differences in RGR throughout the experiment.

Differences in the net photosynthesis response curve for light regime treatments were subjected to analysis of variance with repeated measures (von Ende, 1993). The between-subject main effect was light regime, and the within-subjects or repeated measures effect was irradiance level. Homoscedastic residuals were obtained with untransformed values. No severe departures from the normality assumption were detected by examining half-normal probability plots of z-transformed within-cells correlations. The compound symmetry for the repeated measures ANOVA was not rejected by the Mauchly's sphericity test ( $P=0.11$ ), however, the Huynh-Feldt adjusted significance level (see von Ende, 1993) was used because the epsilon for this test was equal to one, which gives identical adjusted and unadjusted significance levels. *Post hoc* contrasts comparing light regime differences within each irradiance level, were calculated.

## RESULTS

**Biomass allocation-** Light regime effect, assessed by ANOVA, was significant for specific leaf area and leaf area ratio (SLA and LAR;  $F_{1,36} = 302.1$ ,  $P < 0.001$ ) and for stem and root mass values (SMR and RMR, respectively;  $F_{1,36} = 6.32$ ,  $P < 0.02$ ). Mean values (Table 1) for the entire experiment showed that low-light grown *Vismia* had greater, SLA, LAR and SMR and smaller RMR than plants that grew in high light. No significant effect ( $F_{1,36} = 0.07$ ,  $P < 0.8$ ) of light treatments could be detected for LMR (Table 1). The higher values of the leaf area variables (SLA and LAR) for low light grown plants was maintained throughout the experimental period (data not shown). For both regimes the highest SLA and LAR values occurred at the early stages of plant development, declining throughout the experimental period (data not shown).

The proportion of biomass allocated to leaves (LMR) in both light treatments, initially increased up to 15 days and then showed a tendency to decline during the remaining evaluations (data not shown). For both light regimes root mass ratio (RMR) was highest at the beginning of plant development and declined throughout plant growth. Yet, this decline was more pronounced for low-light plants, that experienced a 48 % decrease in RMR between the first and the last evaluation periods, while for high-light plants this decline was only 29 %. Relative

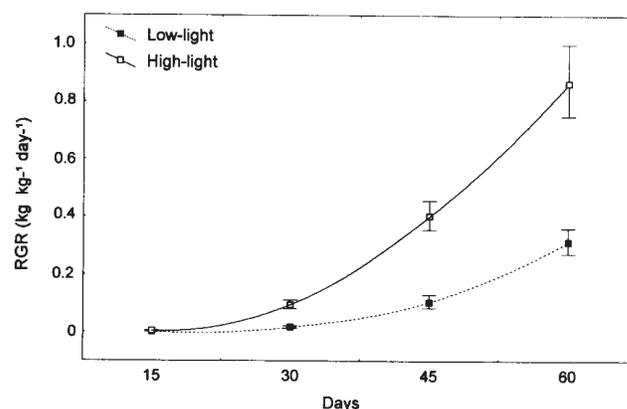
to high-light plants, plants subjected to the low-light treatment allocated a higher proportion of biomass to support tissues (i.e., stem and petiole) (Table 1).

**TABLE 1-** Specific leaf area (SLA,  $m^2 kg^{-1}$ ), leaf area ratio (LAR,  $m^2 kg^{-1}$ ), leaf mass ratio (LMR,  $kg kg^{-1}$ ), stem mass ratio (SMR,  $kg kg^{-1}$ ) and root mass ratio (RMR,  $kg kg^{-1}$ ), as means for the entire experiment (60 days), of *Vismia guianensis* under high- and low-light regimes. Values are means (s.d.),  $n=25$ .

	High-light	Low-light
SLA	29.3 ( 16.4	49.9 ( 12.6
LAR	19.45 ( 0.16	33.27 ( 0.13
LMR	0.665 ( 0.057	0.668 ( 0.052
SMR	0.138 ( 0.033	0.158 ( 0.039
RMR	0.189 ( 0.013	0.165 ( 0.014

**Growth-** The ANOVA for RGR showed a significant Light regime x Time interaction, indicating that RGR was influenced by the light regime treatments. The trend analysis over time (i.e., orthogonal polynomials) suggested that the differences in RGR between the two light treatments was not maintained throughout the entire experimental period, since the quadratic component accounts for the greatest proportion of the interactive effect.

At an early stage of seedling development (i.e., day 15) no difference in RGR could be detected between treatments (Fig. 1). However, throughout the remaining evaluation period high-light grown plants displayed a higher growth rate than low-light grown plants. This difference in RGR increased with time.



**FIGURE 1-** Change over time (days, d) in relative growth rate (RGR) (mean  $\pm$  SE,  $n = 5$ ) of *Vismia* under low- and high-light conditions. The equations adjusted for the growth curves were:

$$RGR = 1.5 + 0.67 d - 0.008 d^2 + 0.003 d^3 \quad \text{low-light}$$

$$RGR = 194.5 - 23.4 d + 0.76 d^2 - 0.003 d^3 \quad \text{high-light}$$

**CO<sub>2</sub> assimilation-** There was a significant Irradiance level x treatment for the within-subjects main effects. No statistically significant differences between light environments and the irradiance response curve could be detected by *post hoc* contrasts. However, at the lowest irradiance level (i.e., 150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) low-light grown plants had a tendency to display a higher mean assimilation rate relative to high-light plants; however, this difference was only marginally significant ( $F_{1,8} = 4.95$ ,  $P > 0.057$ ).

**Photosynthetic parameters-** Light-saturated photosynthesis ( $A_{\text{max}}$ , Fig. 2) was similar between light treatments. Differences between treatments in dark respiration,  $R_d$ , assessed by *post hoc* contrasts showed that high-light grown leaves displayed higher (more negative)  $R_d$  than low-light leaves (mean (s. d.), 0.956 (0.16 versus 0.711 (0.13);  $F_{1,8} = 7.25$ ,  $P < 0.027$ ).

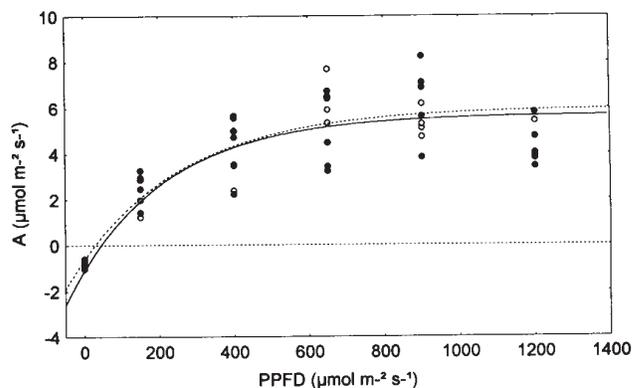
The apparent quantum efficiency,  $\alpha$ , was sensitive to light regime during growth. Low-light plants had a higher ( $t = 2.29$ ,  $P < 0.019$ )  $\alpha$  (mean (s. d.), 0.0236 (0.003) than high-light plants ( $\alpha = 0.0179$  (0.001)). Light compensation point,  $R_d/\alpha$ , was also influenced by the light treatments, being higher ( $t = 3.31$ ,  $P < 0.01$ ) for high-light plants (31.35 (6.1 vs. 52.52 (12.9)).

## DISCUSSION

**Growth and biomass allocation-** The effect of light regime on growth of *Vismia* (Fig. 1) suggests that this species is sensitive to the light environment during growth and that plants grown under shade may have their development considerably suppressed. Although, relative to high-light plants, growth was negatively affected under low irradiance, low-light plants were still able to maintain a positive growth throughout the evaluation period.

Growth, carbon allocation and structure patterns in response to contrasting quantum flux density observed in this study were consistent with the results reported from most studies (e.g., Lambers & Poorters, 1992). Growth under low light promoted an increased SLA and LAR in *Vismia*; yet, allocation to leaves (LMR) was not significantly influenced by development under low quantum flux density (Table 1).

Consistent with previous studies (e.g., Mahall & Schlesinger, 1982; Dall'Armellina & Zindahl, 1988; Zoffinger & Kells, 1991; Thompson et al., 1992a; Walters et al., 1993) the low-light treatment reduced biomass allocation of roots relative to high-light plants. As suggested elsewhere (Thompson et al., 1992a; Walters et al., 1993), this negative effect of low-light regime on biomass allocation to roots is greatest on sun-loving plants and is probably a response to traits that improve carbon gain in low light such as an increased LAR or LMR, or that



**FIGURE 2-** Light response curve of net photosynthesis (A) of *Vismia* grown under low- (closed symbols and dashed lines) and high-light (open symbols and solid lines) conditions. The equations adjusted for the response to the photosynthetic photon flux density (PPFD) were:

$$A = 5.9 [1 - e^{-0.0037(\text{PPFD}-30.5)}] \quad \text{low-light}$$

$$A = 5.7 [1 - e^{-0.0031(\text{PPFD} - 45.4)}] \quad \text{high light}$$

reflect a light seeking strategy such as stem growth. Although in the present study LMR was identical between treatments, mean LAR of low-light *Vismia* was 41 % higher than in high-light plants (Table 1). In addition, low-light plants displayed an overall 13% higher allocation to support tissue (SMR) relative to high-light plants (Table 1).

**Gas exchange response-** The shape of the light response curves in figure 2 suggests a very similar response of low- and high-light grown plants to increasing irradiance levels. However, consistent with observations in other tropical trees (e.g., Ramos & Grace, 1990; Riddoch et al., 1991 a), low-light plants had a tendency to display a higher photosynthetic rate at the lowest irradiance level (150  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ). The photosynthetic features of leaves of low-light *Vismia* suggest that even a shade grown plant of this species is capable of retaining its 'full' photosynthetic capacity.

The higher quantum efficiency observed for low-light plants contrasts with the results reported from similar studies with tropical species (Sims & Pearcy, 1989; Ramos & Grace, 1990; Riddoch et al., 1991a). In these studies it is shown that light regime during growth does not normally alter  $\alpha$  (Fahl et al., 1994). The higher  $\alpha$  observed in low-light *Vismia* can in part explain the tendency for a higher efficiency in CO<sub>2</sub> assimilation observed in low-light plants at the lowest irradiance level (Fig. 2). Also, the lower dark respiration measured in low-light plants may have contributed for the tendency of a higher net photosynthesis observed in low-light plants. The negative effect of a low quantum efficiency on  $R_d$  is a common response that has been observed in other

tropical species (Ramos & Grace, 1990; Riddoch et al., 1991b; Thompson et al., 1992b).

The effect of light treatment on the light compensation point,  $R_d/\alpha$ , reported in the present study followed the same trend observed in other investigations involving tropical species. In these studies low light during growth decreases  $R_d/\alpha$  values (Ramos & Grace, 1990; Thompson et al., 1992b). Here, the lower  $R_d/\alpha$  of low-light plants was derived equally from a low respiration rate and a higher  $\alpha$  observed in low-light plants.

**Ecological and practical implications-** The present results indicate that the light environment has important effects on biomass distribution and growth of *Vismia*. As high-light plants allocated significantly more biomass to roots (Table 1) and had a higher relative growth rate than low-light plants (Fig. 1), *Vismia* was very responsive to the light and could be able to take advantage of the light environment normally found in forest margins, gaps and overgrazed pasture areas in Brazilian Amazonia. Based on these results it appears that plants developed under full sunlight may have an enhanced survivorship in active pasture areas, as a preferential allocation to roots would facilitate resprouting following death of above ground tissues caused by mowing, fire or livestock trampling. Also, as high-light grown *Vismia* allocated a smaller proportion of its biomass to leaf area and a larger proportion to roots than did low-light plants, it could be hypothesized that plants developed under shade could be relatively more vulnerable to edaphic stress factors, such as drought or low nutrient availability due to a comparatively greater transpirational area and a reduced potential for soil moisture and nutrient capture. Moreover, because *Vismia* is known to be capable of vegetative reproduction from root sprouts (Dias-Filho, 1990), low-light conditions may reduce its invasive potential by significantly decreasing the amount of biomass allocated to root tissue.

The photosynthetic data in response to growth under low or high light show that, at least in the short term, low-light grown *Vismia* is capable of satisfactorily responding to increasing irradiance levels. This suggests that *Vismia* is able to retain its full photosynthetic capacity despite growth in shade. On the other hand, high-light grown plants may be to some extent impaired if there is a decrease in the irradiance environment.

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