

PHYSIOLOGICAL RESPONSE OF SOLANUM CRINITUM LAM.

TO CONTRASTING LIGHT ENVIRONMENTS¹

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ABSTRACT - During a 66-day period, a study was made in controlled environment chambers, under high ($800\text{-}1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) and low ($200\text{-}350 \mu\text{mol m}^{-2} \text{s}^{-1}$) light regimes on the physiology, morphology and growth of *Solanum crinitum*, a pioneer medium-sized woody species known to invade forest gaps, active pastures and abandoned agricultural areas in the Brazilian Amazonia. The objective was to investigate the sun-shade acclimation characteristics of this species. High-light grown plants (HL) had higher light saturated rates of photosynthesis than low-light plants (LL). No significant difference in dark respiration was observed between light regimes. Relative growth rate was initially (at 22 d) higher for HL, becoming similar between treatments in the last two harvests (44 and 66 d). Leaf area ratio and specific leaf area were higher for LL. Allocation of biomass to leaves was similar between treatments, while biomass allocated to roots was higher in HL. Allocation of biomass to stems was higher in LL. Leaves grown under high irradiance had less nitrogen per unit of mass and more per unit of area than leaves developed at low irradiance. These results suggest that light is important to the performance of this species and that the differential responses to light conditions may contribute to or detract from its ability to succeed in natural and agricultural environments or to endure control strategies.

Index terms: allocation patterns, growth analysis, photosynthesis, specific leaf area, leaf nitrogen content, Amazonia.

RESPOSTAS FISIOLÓGICAS DE SOLANUM CRINITUM LAM. A DIFERENTES CONDIÇÕES DE LUMINOSIDADE

RESUMO - Investigou-se, durante 66 dias, em câmaras de crescimento, sob alto ($800\text{-}1000 \mu\text{mol m}^{-2} \text{s}^{-1}$) e baixo ($200\text{-}350 \mu\text{mol m}^{-2} \text{s}^{-1}$) regimes de luz, a fisiologia, a morfologia e o crescimento de *Solanum crinitum*, uma espécie arbórea pioneira de porte médio, comum como planta invasora de pastagens, áreas agrícolas abandonadas, e clareiras em áreas de floresta na Amazônia brasileira. O objetivo foi estudar a aclimatação dessa espécie ao sombreamento. A taxa de crescimento relativo foi inicialmente (22 d) similar entre regimes de luz, tornando-se semelhante entre tratamentos nas avaliações subsequentes (44 e 66 d). A razão de área foliar e a área foliar específica foram maiores na BR. A proporção de biomassa alocada nas folhas foi semelhante entre tratamentos, enquanto nas raízes foi maior em AR, e nas hastes e pecíolos foi maior em BR. O conteúdo de nitrogênio foliar por unidade de massa foi maior em BR, ao passo que por unidade de área foi maior em AR. Estes resultados sugerem que o regime de luz é importante para o desempenho dessa espécie, e que as respostas às condições de luminosidade são importantes para que se determine o seu sucesso como planta pioneira em ambientes naturais ou planta invasora de ambientes agrícolas.

Termos para indexação: alocação de biomassa, análise de crescimento, fotossíntese, nitrogênio foliar, Amazônia.

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INTRODUCTION

The nature of the photomorphogenic responses to the light environment (quantity and quality of light) is dependent on the plasticity of the plant (i.e., acclimation capacity) (Clough et al., 1979; Walters & Field, 1987; Givnish, 1988; Seemann, 1989; Woodward, 1990). The ability of an individual species to successfully grow in a low or high light environment (holding quality constant) can be based on how rapidly and how efficiently allocation patterns and physiological behavior are adjusted in order to maximize resource acquisition in that particular environment.

Knowing how plant species respond morphologically and physiologically to contrasting light conditions can be critical in helping to explain and predict their occurrence and abundance patterns under specific environmental conditions. For successional and weed species, this information can be useful to understand the successional process and to explain their invasive potential and competitive ability under different management situations in cultivated areas. Ultimately this information can help in the development of more effective control practices.

The present study involved work with *Solanum crinitum* Lam. (Solanaceae) a native early successional small tree (around 2 m) species from tropical America found as colonizer of man-made clearings and natural gaps in forests and in abandoned or active agricultural and pasture areas in the Brazilian Amazonia (Albuquerque, 1980; Dantas, 1989; Dias-Filho, 1990). The purpose of this study was to investigate the sun-shade acclimation characteristics of this species.

MATERIAL AND METHODS

Plant material and growing conditions

Solanum crinitum seeds were collected from plants growing in pasture areas near Paragominas PA ($3^{\circ} 5' S$ and $47^{\circ} 21' W$) in the eastern Brazilian Amazonia. Seeds were germinated on filter paper in 9 cm petri dishes and then planted individually in 1750 mL plastic pots in a mixture of peat:vermiculite:perlite (1:1:1). Plants were initially grown in a greenhouse at temperatures of $24 \pm 2.2^{\circ}C$ (minimum) to $33 \pm 2.1^{\circ}C$ (maximum) and a maximum photosynthetic photon flux density (PPFD) of approximately $1000 \mu\text{mol m}^{-2} \text{s}^{-1}$. When plants were about 25 days old they were transferred from the greenhouse to two Conviron growth chambers (Model PGW36. Controlled Environments, Inc. Pembina, ND) set at $28/24^{\circ}C$ day/night air temperatures, 70% relative humidity, and 12 h photoperiod. Before transference to the growth chambers, seedlings were divided into five size classes, and each class was randomly assigned to a replication (block).

Within each growth chamber, 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 each growth chamber. Irradiance, monitored throughout the experiment with a light 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 200 and $350 \mu\text{mol m}^{-2} \text{s}^{-1}$ for low-light treatments.

All pots were watered daily to full capacity with deionized water and fertilized every 11 days with 50 mL per pot of a water soluble fertilizer solution (15% N, 30% P₂O₅, 15% K₂O, 0.02% B, 0.07% Cu, 0.15% Fe, 0.05% Mn, 0.0005% Mo and 0.06% Zn; 3.5 g L⁻¹).

Growth analysis

Four harvests were made; the first harvest was on the day plants were transferred to the growth chambers (Day 0), and the other 22, 44 and 66 days later (n= 5 per harvest and light treatment). At each harvest, plant material was divided into leaf, support tissue (stem and petiole) and root. Leaves were removed and leaf area measured using a leaf area meter (Model LI-3000. Li-Cor, Inc. Lincoln, NE) and conveyor belt assembly (Model LI-3050. Li-Cor, Inc. Lincoln, NE). Plant dry mass was obtained by drying the plant material in an oven at $73^{\circ}C$ for 48 hours. Attributes measured for each plant at each harvest were used to estimate relative growth rate (change in dry mass per total dry mass of plant per day, RGR) and biomass allocation patterns: leaf area ratio (ratio between total leaf area per plant and total dry mass per plant, LAR), specific leaf area (ratio between total leaf area per plant and total leaf dry mass per plant, SLA) and leaf, stem and root mass ratios (respectively, the ratio between total leaf, stem or root dry mass per plant and total dry mass per plant, LMR, SMR and RMR). All of the above growth and biomass allocation parameters were calculated according to Hunt (1990).

Gas exchange

Gas exchange parameters were measured on plants just before the fourth harvest, i.e., when the plants had been in the growth chamber for 66 days. A photosynthesis (A) versus light (PPFD) response curve (starting at ca. 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and decreasing in five steps to 0), was measured in the laboratory on the most recent, fully expanded intact leaf of all plants using a portable photosynthesis system (Model LI-6200, LI-COR, Inc., Lincoln, NE). Gas exchange parameters were calculated on a leaf area basis. The amount of leaf area in the chamber (cuvette) was approximately 20 cm^2 . The 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 were made after an adjustment period of about 15 min to each new light level. To absorb long-wave radiation and maintain constant leaf temperatures in the cuvette, a 10 cm deep Plexiglas circulating bath of cool water was suspended between the light source and the leaf cuvette. After exposure to the lowest PPFD, plants were left for 20 min in the dark, and measurements were made to obtain 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 mol^{-1} .

Photosynthesis versus light response data provided direct estimates of the highest measured value of photosynthetic rate (A_{\max}). Apparent quantum yield of CO_2 to incident light (α) was calculated according to Thompson et al. (1992a): 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 CO_2 exchange, for each light regime combination. The light compensation point was calculated as the ratio, R_d/α .

Leaf nitrogen analysis

Leaf nitrogen was measured on all leaves of each individual plant at each harvest date and light treatment combination. Leaf nitrogen content was measured with a nitrogen analyzer (Model NA 1500, series 2. Carlo Erba Strumentazione, Milan, Italy). The instrument was calibrated with both an NBS “citrus leaf” and organic standard. Precision was $\pm 0.17\%$ of N.

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 environmental 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 \times Time interaction in an ANOVA with logarithmically-transformed dry mass as dependent variable (Poorter & Lewis, 1986). A trend analysis over time was performed to detect differences in RGR throughout the experiment. The statistical packages MINITAB, Release 9.2 for Windows (MINITAB, 1993) and SYSTAT Version 5.03 (Wilkinson, 1990) were used for the computations of the growth and biomass allocation data.

Differences in net photosynthesis and stomatal conductance response curves for species and light treatments were analyzed by multivariate analysis of variance (MANOVA) with repeated measures. The multivariate approach was preferred over its univariate counterpart because, in the latter, the compound symmetry of the covariance matrix was rejected for the data, and there was never total agreement between the Huynh-Feldt and the Greenhouse-Geisser corrected significance levels (Von Ende, 1993). The between-subject main effects were species and light regimes, and the within-subject or repeated measures effect was light level. No severe departures from the normality assumption were identified by examining half-normal probability plots of z-transformed within-cell correlations for both data sets. Post hoc contrasts were calculated comparing species and light regimes differences in photosynthesis and stomatal conductance, within each irradiance level, and pooling all irradiance levels. The statistical package STATISTICA for Windows release 4.5 (Statistica..., 1994) was used for all computations of the data.

RESULTS AND DISCUSSION

Biomass allocation and growth

Both specific leaf area and leaf mass ratio were significantly increased ($P = 0.001$) by shade (Table 1). Mean values for the entire experimental period showed that low-light plants allocated significantly less biomass in root tissue and more biomass in support tissues (stem and petiole). However, no significant difference between light treatments could be detected in the mean proportion of biomass allocated to leaves.

TABLE 1. Specific leaf area (SLA, $\text{m}^2 \text{ kg}^{-1}$), leaf area ratio (LAR, $\text{m}^2 \text{ kg}^{-1}$), 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 d), of *Solanum crinitum* under high- and low-light regimes. Values are means ($\pm \text{s.e.}$)¹, n=20.

Parameter	High-light	Low-light
A_{\max} ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	6.45	3.35
α ($\text{mol CO}_2 \text{ photon}^{-1}$)	0.023 (0.004)	0.022 (0.004)
R_d ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	2.76 (0.21)	2.81 (0.43)
R_d/a ($\mu\text{mol m}^{-2} \text{ s}^{-1}$)	123.1 (17.8)	128.1 (15.0)

Patterns of biomass allocation throughout the experimental period were distinct between treatments (Fig. 1). In low-light plants, the proportion of biomass allocated to leaves (LMR) declined steadily through time while in high-light plants a quadratic pattern was observed, with LMR declining between days 22 and 44 and increasing at day 66.

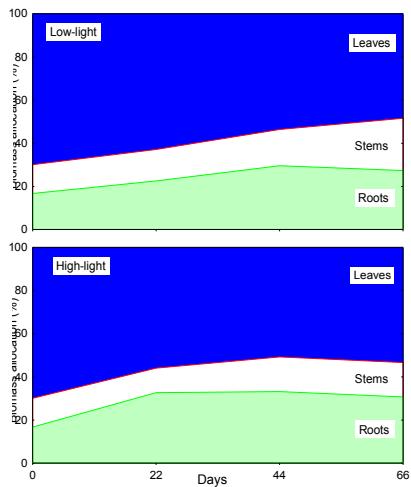
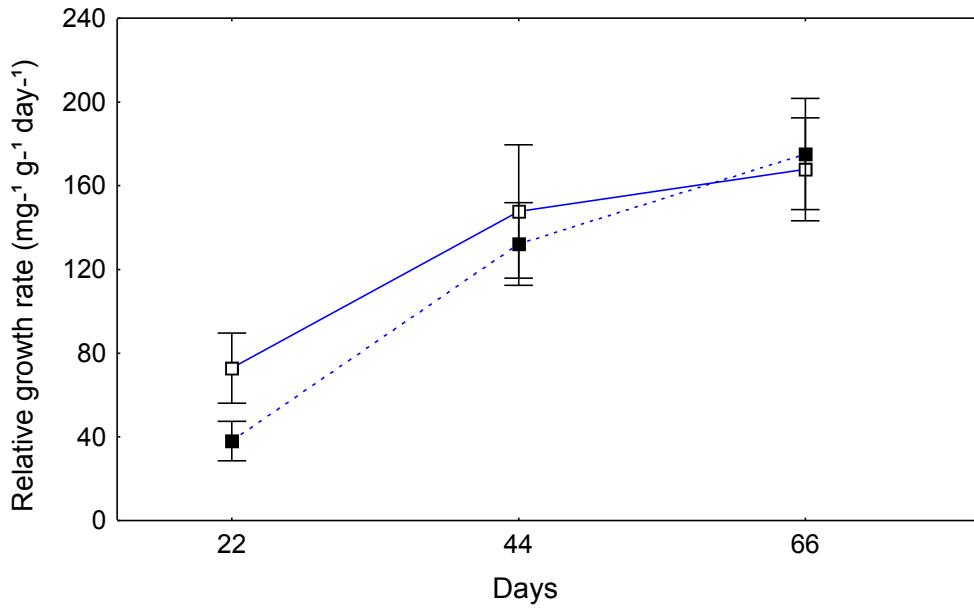


FIG. 1. Mean proportion of biomass allocated to roots, stems and leaves as a function of time and light environment in *Solanum*.

The proportion of biomass allocated to support tissue (SMR) was relatively constant through time in high-light plants, however, in low-light plants, SMR had a tendency to increase between days 44 and 66 (Fig. 1).

In both treatments, allocation of biomass to roots started to decline after day 44, yet, this decline was relatively more pronounced in low-light plants. Comparatively, however, high-light plants always allocated a



higher proportion of biomass to roots.

The results of the ANOVA showed that no statistical difference could be detected for the interaction between Time and Treatments (light regimes). This suggests that mean RGR in *Solanum* was not significantly influenced by the light regimes. However, high-light plants showed a tendency for a higher growth rate throughout most of the experimental period, losing this superiority at the last evaluation period (Fig. 2).

FIG. 2. Change over time in relative growth rate (mean \pm s.e., $n = 5$) of *Solanum* under low- (closed symbol and dashed line) and high-light (open symbol and solid line) conditions.

A common response to shade reported in many studies is a reduced allocation to roots (Mahall & Schlesinger, 1982; Dall'Armellina & Zimdahl, 1988; Zollinger & Kells, 1991; Dale & Causton, 1992; Messier, 1992; Thompson et al., 1992b; Walters et al., 1993). In the present study, allocation to roots in low-light *Solanum* (averaged over the entire experimental period) was reduced by 15% relative to high-light plants (Table 1). As suggested elsewhere (Thompson et al., 1992b; Walters et al., 1993), this lower allocation

to roots under low light conditions is known to be maximized in sun-loving plants, and probably reflect a response to attributes that improve carbon gain under reduced irradiance such as an increase in LAR and LMR, or that reflect a light seeking strategy such as an increase in height. Although no significant difference between treatments could be detected in LMR, low-light plants had indeed a 33% higher mean LAR than high-light plants (Table 1), and also, at the last evaluation date, were 26% higher than high-light plants ($t = 2.7$, $P = 0.03$).

The significantly lower specific leaf area (SLA, Table 1) in high-light Solanum suggests leaf anatomical differences brought about by low quantum flux density (Lambers & Poorter, 1992), and reflects a strategy to increase this species competitive ability under low light through an increase in leaf area. An increase in SLA is a common response observed in plants under low light conditions (George & Nair, 1990; Ducrey, 1992; Buisson & Lee, 1993; Stoneman & Dell, 1993; Fahl et al., 1994) and is usually associated with extra layers of mesophyll cells (Riddoch et al., 1991b; Thompson et al., 1992b).

The growth patterns observed in Fig. 2 suggest that Solanum seedlings were able to maintain relative growth rate (RGR) under low-light conditions to levels comparable to that of high-light plants. As suggested for herbaceous plants (Björkman, 1981), it could be speculated that in low-light Solanum, the significant adjustment in LAR may have in part contributed to partially offset light-limited photosynthesis so that the whole-plant RGR was less affected.

CO₂ assimilation and photosynthesis parameters

Results from the repeated measures MANOVA showed significant irradiance levels \times treatments differences in CO₂ assimilation. There was also a significant treatment main effect difference in CO₂ assimilation.

In general, leaves from high-light plants had higher photosynthetic capacity than low-light leaves. Post hoc contrasts revealed significant differences between treatments in the irradiance response curve at the first (ca. 1500 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 39.7$, $P < 0.001$), second (ca. 900 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 64.8$, $P < 0.001$), third (ca. 650 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 6.0$, $P = 0.04$) and fourth (ca. 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$, $F_{1,8} = 9.8$, $P = 0.01$) irradiance levels. High-light grown plants had higher CO₂ assimilation rates at these irradiance levels (Fig. 3).

No significant difference between treatments in CO₂ assimilation could be detected at the lowest irradiance level (ca. 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$, Fig. 3).

The shape of the light response curve of photosynthesis (Fig. 3) indicates that the light saturation points of both treatments were very close to the actual maximum PPFD received during growth.

No significant difference between treatments could be detected in dark respiration (Table 2). Dark respiration values in Solanum were much higher than the ones reported for other tropical species (Ramos & Grace, 1990; Riddoch et al., 1991b; Thompson et al., 1992a). A high respiration is characteristic of leaves with high rates of expansion and short life spans (Thompson et al., 1992a). Although there is no information on Solanum leaf life span, this species does have a high leaf expansion rate.

As a consequence of the higher dark respiration measured in Solanum, the light compensation point calculated for this species on both treatments was also very high (Table 2). No significant difference between treatments could be detected for this parameter. It could be speculated that the high light compensation point of Solanum would make this species more prone for recruitment in wide disturbance gaps, such as the ones characteristic of most anthropogenic disturbances in Brazilian Amazonia.

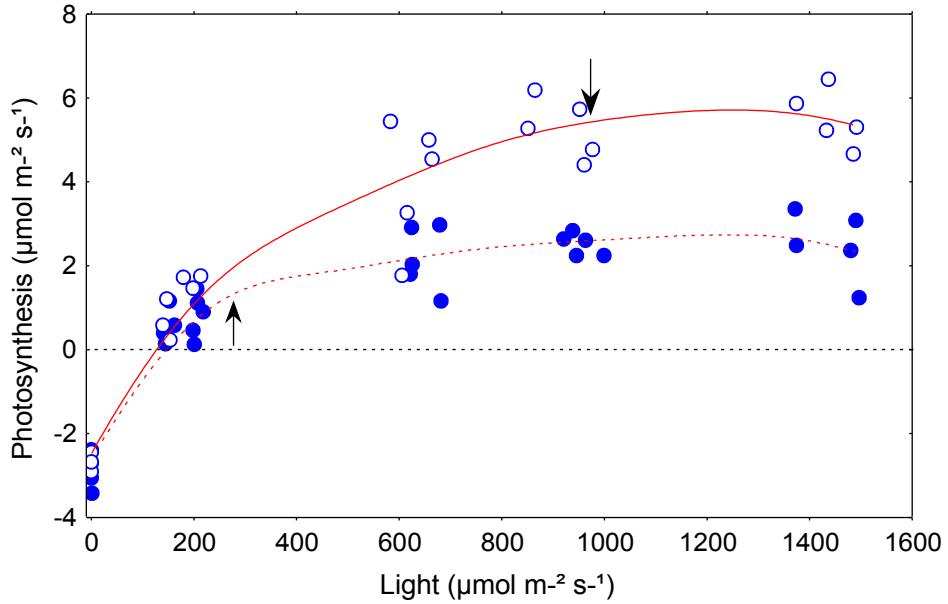


FIG. 3. Light response curve of photosynthesis of *Solanum* grown under low- (closed symbol and dashed line) and high-light (open symbol and solid line) conditions. Curves fitted by distance-weighted least squares.

TABLE 2. Photosynthetic parameters of *Solanum crinitum* under high- and low-light regimes. A_{\max} is light saturated photosynthesis rate; α is apparent quantum efficiency; R_d is dark respiration and R_d/α is light compensation point. Values are means (\pm sample s.d.), n=5.

Parameter	High-light	Low-light
A_{\max} ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	6.45	3.35
α ($\text{mol CO}_2 \text{ photon}^{-1}$)	0.023 (0.004)	0.022 (0.004)
R_d ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	2.76 (0.21)	2.81 (0.43)
R_d/α ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	123.1 (17.8)	128.1 (15.0)

Consistent with the responses observed from other similar studies with tropical species (Sims & Pearcy, 1989; Ramos & Grace, 1990; Riddoch *et al.*, 1991b; Wiebel *et al.*, 1993) the quantum efficiency did not differ significantly between treatments. The α derived for *Solanum* was similar to the ones reported by Riddoch *et al.* (1991a) for some tropical pioneer trees and by Wiebel *et al.* (1993) to the tropical tree *Gracinia mangostana*.

Light-saturated photosynthesis (A_{\max} , Table 2, Fig. 3) was higher for high light plants. For all other photosynthetic parameters shown in Table 2 no statistically significant difference could be detected between treatments. However, low-light plants had a tendency to display higher values of dark respiration and light compensation point.

Nitrogen content

Nitrogen content per unit of leaf mass was significantly higher ($F_{1,22} = 8.5, P = 0.008$) in plants developed at low light (Fig. 4). When expressed on an area basis, however, leaf nitrogen was significantly higher ($F_{1,22} = 14.6, P = 0.001$) in plants grown under high-light. This response followed the same pattern reported for other studies with tropical species (Thompson et al., 1992b; Fahl et al., 1994)

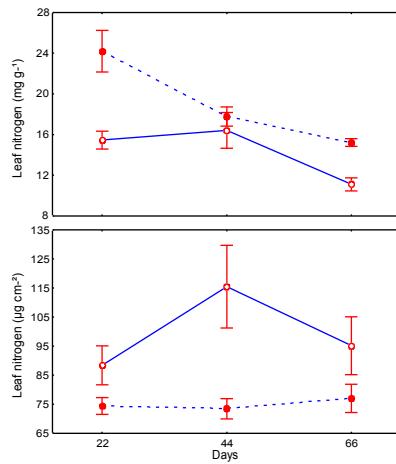


FIG. 4. Leaf nitrogen content (mean \pm s.e., $n=4$) on a mass (mg g^{-1}) and area ($\mu\text{g cm}^{-2}$) basis for *Solanum* under low- (closed symbol and dashed line) and high- (open symbol and solid line) light conditions.

CONCLUSIONS

1. *Solanum crinitum* has the ability to develop morphological and physiological adjustment responses that, in part, can offset loss of photoassimilate under low light and, as a consequence, maintain growth to satisfactory levels.

2. The biomass allocation response of this species to shade, characterized by a higher carbon investment in above ground tissues relative to roots, might render low-light *Solanum* more vulnerable to stresses that directly affect its above ground tissue such as fire, herbivory or mowing.

REFERENCES

- ALBUQUERQUE, J.M. Identificação de plantas invasoras de cultura da região de Manaus. **Acta Amazonica**, v.10, p.47-95, 1980.
- BJÖRKMAN, O. Responses to different quantum flux densities. In: LANGE, O.L.; NOBEL, P.A.; OSMOND, C.B.; ZIEGLER, H. (Eds.). **Physio-logical plant ecology**. Berlin: Springer-Verlag, 1981. p.57-107. (Encyclopedia of Plant Physiology, 12A)
- BUISSON, D.; LEE, D.W. The developmental responses of papaya leaves to simulated canopy shade. **American Journal of Botany**, v.80, p.947-952, 1993.
- CLOUGH, J.M.; TEERI, J.A.; ALBERTE, R.S. Photosynthetic adaptation of *Solanum dulcamara* L. to sun and shade environments. **Oecologia**, v.38, p.13-21, 1979.
- DALL'ARMELLINA, A.A.; ZIMDAHL, R.L. Effect of light on growth and development of field bindweed (*Convolvulus arvensis*) and Russian knapweed (*Centaurea repens*). **Weed Science**, v.36, p.779-783, 1988.
- DALE, M.P.; CAUSTON, D.R. The ecophysiology of *Veronica chamaedrys*, *Veronica montana* and *Veronica officinalis*. II. The interaction of irradiance and water regime. **Journal of Ecology**, v.80, p.493-504, 1992.
- DANTAS, M. **Studies on succession in cleared areas of Amazonia rain forest**. Oxford: Oxford Univ., 1989. 397p. Ph.D. Thesis.
- DIAS-FILHO, M.B. **Plantas invasoras em pastagens cultivadas da Amazônia: estratégias de manejo e controle**. Belém: Embrapa-CPATU, 1990. 103p. (Embrapa-CPATU. Documentos, 52)
- DUCREY, M. Variation in leaf morphology and branching pattern of some tropical rain forest species from Guadeloupe French West Indies under semi-controlled light conditions. **Annales des Sciences Forestieres**, v.49, p.553-570, 1992.
- FAHL, J.I.; CARELLI, M.L.C.; VEGA, J.; MAGALHÃES, A.C. Nitrogen and irradiance levels affecting net photosynthesis and growth of young coffee plants (*Coffea arabica* L.). **Journal of Horticultural Science**, v.69, p.161-169, 1994.
- GEORGE, S.; NAIR, R.V. Effect of shading on leaf development and chlorophyl content in groundnut (*Arachis hypogaea* L.). **Legume Research**, v.13, p.130-132, 1990.
- GIVNISH, T.J. Adaptation to sun and shade: a whole-plant perspective. **Australian Journal of Plant Physiology**, v.15, p.63-92, 1988.
- HUNT, R. **Basic growth analysis: plant growth analysis for beginners**. London: Unwin Hyman, 1990. 112p.
- LAMBERS, H.; POORTER, H. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. **Advances in Ecological Research**, v.23, p.187-261, 1992.
- MAHALL, B.E.; SCHLESINGER, W.H. Effects of irradiance on growth, photosynthesis, and water use efficiency of seedlings of the Chaparral shrub, *Ceanothus megacarpus*. **Oecologia**, v.54, p.291-299, 1982.
- MESSIER, C. Effects of neutral shade and growing media on growth biomass allocation and competitive ability of *Gaultheria shallon*. **Canadian Journal of Botany**, v.70, p.2271-2276, 1992.
- MINITAB. **Reference manual, release 9 for windows**. State College, PA, 1993.
- POORTER, H.; LEWIS, C. Testing the differences in relative growth rate: a method avoiding curve fitting and pairing. **Physiological Plantarum**, v.67, p.223--226, 1986.

- RAMOS, J.; GRACE, J. The effects of shade on gas exchange of seedlings of four tropical trees from Mexico. **Functional Ecology**, v.4, p.667-677, 1990.
- RIDDOCH, I.; GRACE, J.; FASEHUN, F.E.; RIDDOCH, B.; LAPIDO, D.O. Photosynthesis and successional status of seedlings in a tropical semi-deciduous rain forest in Nigeria. **Journal of Ecology**, v.79, p.491-503, 1991a.
- RIDDOCH, I.; LEHTO, T.; GRACE, J. Photosynthesis of tropical tree seedlings in relation to light and nutrient supply. **New Phytologist**, v.119, p.137-147, 1991b.
- SEEMANN, J.R. Light adaptation/acclimation of photosynthesis and the regulation of ribulose-1,5-bisphosphate carboxylase activity in sun and shade plants. **Plant Physiology**, v.91, p.379-386, 1989.
- SIMS, D.A.; PEARCY, R.W. Photosynthetic characteristic of a tropical forest understory herb *Alocasia macrorrhiza* and a related crop species, *Colocasia esculenta* grown in contrasting light environments. **Oecologia**, v.79, p.55-59, 1989.
- STATISTICA for windows general conventions and statistics I. Tulsa: StatSoft, 1994. v.1, 717p.
- STONEMAN, G.L.; DELL, B. Growth of *Eucalyptus marginata* (Jarrah) seedlings in a greenhouse in response to shade and soil temperature. **Tree Physiology**, v.13, p.239-252, 1993.
- THOMPSON, W.A.; HUANG, L.-K.; KRIEDEMANN, P.E. Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees. II. Leaf gas exchange and component processes of photosynthesis. **Australian Journal of Plant Physiology**, v.19, p.19-42, 1992a.
- THOMPSON, W.A.; KRIEDEMANN, P.E.; CRAIG, I.E. Photosynthetic response to light and nutrients in sun-tolerant and shade-tolerant rainforest trees. I. Growth, leaf anatomy and nutrient content. **Australian Journal of Plant Physiology**, v.19, p.1-18, 1992b.
- VON ENDE, C.N. Repeated-measures analysis: growth and other time-dependent measures. In: SCHEINER, S.M.; GUREVITECH, J.G. (Eds.). **Design and analysis of ecological experiments**. New York: Chapman and Hall, 1993. p.113-137.
- WALTERS, M.B.; FIELD, C.B. Photosynthetic light acclimation in two rainforest Piper species with different ecological amplitudes. **Oecologia**, v.72, p.449-456, 1987.
- WALTERS, M.B.; KRUGER, E.L.; REICH, P.B. Growth, biomass distribution and CO₂ exchange of northern hardwood seedlings in high and low light: relationships with successional status and shade tolerance. **Oecologia**, v.94, p.7-16, 1993.
- WIEBEL, J.; EAMUS, D.; CHACKO, E.K.; DOWNTON, W.J.S.; LUDDERS, P. Gas exchange characteristics of mangosteen *Gracinia mangostana* L. leaves. **Tree Physiology**, v.13, p.55-69, 1993.
- WILKINSON, L. **SYSTAT**: The system for statistics. Evanston, IL: SYSTAT Inc., 1990. 677p.
- WOODWARD, F.I. From ecosystems to genes: the importance of shade tolerance. **Tree**, v.5, p.111-115, 1990.
- ZOLLINGER, R.K.; KELLS, J.J. Effect of soil pH, soil water, light intensity, and temperature on perennial sowthistle (*Sonchus arvensis* L.). **Weed Science**, v.39, p.376-384, 1991.