Acta Scientiarum
http://www.uem.br/acta
ISSN printed: 1679-9283
ISSN on-line: 1807-863X
Doi: 10.4025/actascibiolsci.v37i3.28179

Influence of light on the initial growth of invasive *Cryptostegia madagascariensis* Bojer in the Brazilian semiarid region

Selma Freire de Brito[1*], Charles Lobo Pinheiro[1], Francisco Carlos Barboza Nogueira[2], Sebastião Medeiros Filho[1] and Dalva Maria da Silva Matos[3]

*[1]Laboratório de Análise de Sementes, Departamento de Fitotecnia, Universidade Federal do Ceará, 60356-001, Fortaleza, Ceará, Brazil. [2]Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais Renováveis, Fortaleza, Ceará, Brazil. [3]Departamento de Hidrobiologia, Universidade Federal de São Carlos, São Carlos, São Paulo, Brazil. *Author for correspondence. E-mail: crselma@hotmail.com*

ABSTRACT. The invasion by *Cryptostegia madagascariensis* causes economic and environmental problems in Northeastern Brazil. Current study evaluates the initial growth of *C. madagascariensis* on light gradient. The experiment used 0, 30, 50 and 70% shading treatments arranged in a completely randomized design and evaluated in four periods, namely, 35, 50, 65 and 80 days. Height, absolute growth rate, relative growth rate, number of side branches, number of leaves, leaf area, specific leaf area, leaf area ratio, root mass ratio, stem mass ratio, leaf mass ratio and leaf area/root mass ratio were evaluated. Results showed that the height was greater in shade environments, and the greater the available light, the greater was the number of side branches. *C. madagascariensis* is able to change the leaf area, specific leaf area and biomass allocation in different shadings. Since *C. madagascariensis* varies growth forms and performs morphological adjustments to increase light uptake, the plant has warranted success during the initial growth under different shadings.

Keywords: functional traits, Caatinga, shading, morphological adjustments, biomass.

Influência da luz no crescimento inicial da invasora *Cryptostegia madagascariensis* Bojer no semiárido Brasileiro

RESUMO. A invasão da *Cryptostegia madagascariensis* causa problemas econômicos e ambientais no Nordeste do Brasil. O objetivo do trabalho foi estudar o crescimento inicial da *C. madagascariensis* em gradiente de luz. O experimento utilizou os tratamentos de 0, 30, 50 e 70% de sombreamento, dispostos em um delineamento experimental inteiramente casualizado e avaliados em quatro períodos: 35, 50, 65 e 80 dias. Foram avaliados a altura, a taxa de crescimento absoluto, a taxa de crescimento relativo, o número de ramos laterais e de folhas, a área foliar, a área foliar específica, a razão de área foliar, a razão de massa da raiz, a razão de massa do caule, a razão de massa das folhas e a razão área foliar/massa da raiz. Os resultados mostraram que a altura foi maior em ambientes sombreados e, quanto mais luz disponível, maior o número de ramos laterais. A *C. madagascariensis* é capaz de alterar a área foliar, a área foliar específica e na alocação de biomassa nos diferentes sombreamentos. Portanto, a *C. madagascariensis* varia a forma de crescimento e realiza ajustes morfológicos para aumentar a captação de luz, o que garantiu seu sucesso durante o crescimento inicial em diferentes sombreamentos.

Palavras-chave: características funcionais, Caatinga, sombreamento, ajustes morfológicos, biomassa.

Introduction

Invasive plants direct and indirect impact ecosystems (WEIDENHAMER; CALLAWAY, 2010) and the analysis of different abiotic factors such as light, temperature and water availability that interfere with the invasiveness of new areas triggers to in-depth knowledge on the invasion process (THEOHARIDES; DUKES, 2007; GUREVITCH et al., 2008) and on the risks of new invasions. In general, environments with more resources, such as water, light and nutrients, are more prone to invasion (DAVIS et al., 2000).

Light availability is one of the most important resources for plants, and their responses to light availability variations are critical to assess the invasiveness in different areas (FUNK, 2013). The Caatinga is a deciduous forest of the Brazilian Northeastern semiarid region, plants shed off their old foliage during the dry season, whilst new growth begins at the start of the rainy season, causing variations in light availability (BARBOSA, 2003). Studies on deciduous forest species under different shading conditions demonstrate that light does not affect the species survival, but it affects their growth, biomass allocation and physiological responses (PHONGUODUME et al., 2012; FERREIRA et al., 2012).

Similarly, studies on invasive plants show that they are efficient in adapting biomass and in making physiological adaptations under different light availabilities (ZHENG et al., 2009; FUNK; ZACHARY, 2010; QIN et al., 2012; ZHENG et al., 2012). Therefore, they respond better than some native species in places with greater light supply (GUREVITCH et al., 2008). The ability to adapt to changes in the resource supply is associated with phenotypic plasticity (FUNK, 2008), which is an important strategy that increases invasiveness and allows invasive species to colonize different environments (GODOY et al., 2012; ZENNI et al., 2014).

Cryptostegia madagascariensis Bojer (Apocynaceae) is an invasive plant in Australia and in Northeastern Brazil. It develops successfully as a shrub when growing alone in open areas; however, when it grows near native species, its branches cover all the surrounding trees and lead them to death (SILVA et al., 2008). In Brazil, this invasive shrub is mainly associated with areas of occurrence of *Copernicia prunifera* (Mill.) H. E. Moore, a palm tree that plays an important economic role in the region. In fact, the invasion of *C. madagascariensis* threatens its survival since may kill it (SILVA et al., 2008). *C. madagascariensis* may be found in dry forests, savanna, pastures and disturbed areas, usually growing in full sun light (SILVA et al., 2008). Thus, its success as an invasive plant may depend on its phenotypic plasticity to different light availabilities and on its efficient use of resources. Current paper raises the hypothesis that *C. madagascariensis* exhibits phenotypic plasticity by changing its form of growth and biomass allocation during its initial growth according to light availability.

Current study evaluates the initial growth of *C. madagascariensis* in a light gradient so that the following questions may be answered: 1) Does the growth rate of plants obtained from the same cohort vary according to luminosity? 2) Do plants exhibit morphological changes when they grow under different light conditions? 3) Do these morphological changes lead to differences in biomass investment? The assessment of how shading affects the establishment of *C. madagascariensis* will identify the risk of invasion in different environments, if one takes into consideration the ecological and economic impact caused by the species on the semiarid region.

Material and methods

Studied specie and seed collection

Cryptostegia madagascariensis, popularly known in the State of Ceará, Brazil, as *unha-do-diabo* (devil's nail) or *viuvinha alegre* (cheerful widow), is native to Madagascar (Africa) and is part of a list of plants considered potentially invasive in the Caatinga (CAVALCANTE; MAJOR, 2006). One of the areas invaded by this species is the Experimental Farm Vale do Curu, (3°47'S; 39°16'W) of the Federal University of Ceará (UFC) and located in Pentecoste County, State of Ceará, Brazil. The farm lies in the Brazilian semiarid region, with average annual rainfall 772.2 mm, according to data from the local weather station.

Plant material, harvested from the farm to identify the species, was taken to the Herbarium Prisco Bezerra – EAC UFC and deposited under voucher number 54608 (EAC). The ripe fruit of *C. madagascariensis* was collected in February 2013, packed in plastic bags and transported to the Seeds Laboratory of the UFC where they were processed. Seeds were stored in a cold chamber at 10°C and 60% relative humidity (RH) for 2 months until the beginning of the experiment which was conducted under different light availabilities at the Didactic Center for Agricultural Sciences, Plant Science Department, Federal University of Ceará.

Initial growth in light gradient

Seedlings were obtained by sowing in 128-cell trays. They were kept in a greenhouse with 30% shading and watered daily. After germination, the seedlings, featuring a pair of leaves, were randomly selected and transferred to polyethylene bags (18 x 28 cm) containing soil and humus at a volumetric ratio of 3:1. The seedlings were placed in wooden structures (3 m wide x 6 m long) covered with nylon screen, which provided 30, 50 and 70% shading from sunlight, according to the manufacturer's specifications. For 0% shading condition, an area without any coverage was used. Forty-eight plants were distributed for each treatment, with a total of 192 plants for the experiment.

Assay design was completely randomized, with four replications for each of the four types of shading (0, 30, 50 and 70%), and the seedlings were evaluated at four time intervals (35, 50, 65 and 80 days after transplantation). The seedlings were irrigated daily and the position of the seedlings was randomly rearranged within each repetition at every 15 days. Temperature and relative humidity (RH) were measured by a thermo-hygrometer in each shading environment, with the following mean rates during the experiment period: 28.7°C and RH 62.1% (0% shading); 31.1°C and RH 56.1% (30% shading); 30.1°C and RH 57.6% (50% shading); 29.8°C and RH 56.5% (70% shading).

Measurements

Twelve plants were randomly selected from each treatment in each evaluation, with three plants to each replication. The plants were removed from the bags with flowing water not to damage the roots. Stem height, number of leaves and the number of side branches were measured. The leaf area was determined by using the leaf area meter, model LI-3100C, LI-COR. Plants were divided into root, stem and leaf, dried at 80°C for 24 hours and weighed to evaluate their biomass. Specific leaf area (SLA), leaf area ratio (LAR), leaf area/root mass ratio (LA/RM), root mass ratio (RMR), stem mass ratio (SMR) leaf mass ratio (LMR) and absolute growth rate (AGR) and relative growth rate (RGR) were then calculated (POORTER; WERF, 1998; POORTER, 1999).

Statistical analysis

The differences between the studied variables were analyzed according to different treatments and at different time intervals by ANOVA, whilst averages were compared by Tukey's test at 5% significance level. Kolmogorov-Smirnov and Watson test was employed to analyze the distribution normality. Data were given by bar graphs; the relationship between variables was analyzed by Pearson's correlation test; and data were presented in a correlation graph. Graphs and their analyses were designed on Sigmaplot 11.0 statistical software.

Results

Morphological features and biomass allocation

No seedling mortality occurred in any of the shading treatments during the experiment, and the interaction between shading and time was significant in all variables at 1% significance. Plant height was higher when light availability was reduced, thus increasing each evaluation period. Lowest heights were reported at 0% shading in all assessments. Eighty days after the start of the treatments, the plants with 0% shading measured approximately 60 cm, whereas shaded plants were higher than 90 cm. Eighty days after, greatest heights were found at 30 and 50% shadings (Figure 1A).

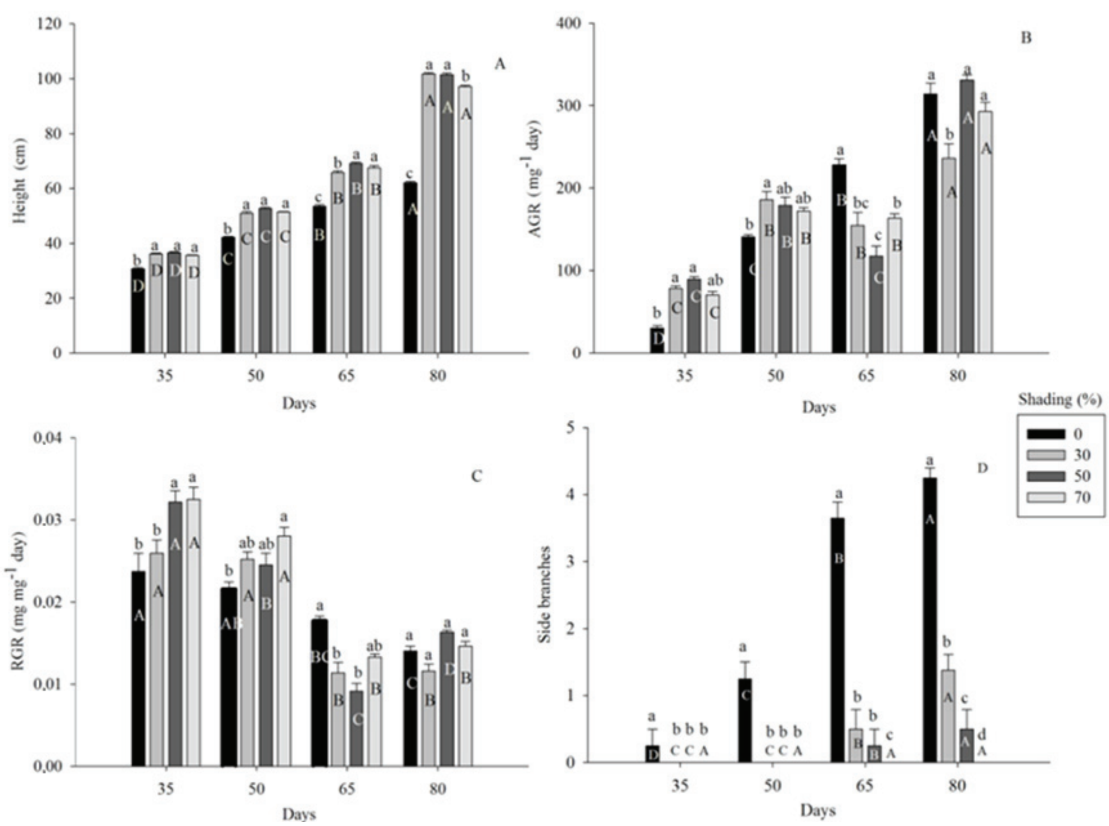

Figure 1. Height (A), absolute growth rate (AGR) (B), relative growth rate (RGR) (C) and numbers of side branches (D) of *Cryptostegia madagascariensis* growing at four shading levels. Shades with the same lower case letter did not differ for the same period; those with the same capital letter did not differ among the evaluation periods.

AGR increased over time and in all shadings between 65 and 80 days. In the first evaluation, AGR rates revealed that plants exposed to 0 and 70% shading had a lower growth, whereas rates were highest in 0, 50 and 70% shadings at 80 days (Figure 1B). Although AGR increased over time, RGR decreased during the experiment and there were no differences among the shadings after 80 days of treatment (Figure 1C).

Shading reduced the number of side branches and extended their formation time. The plants under 70% shading did not produce side branches up to 80 days of treatment. When plants under 0% shading were taken into account, the formation of side branches was reported 35 days after the start of the treatment, whereas plants under 30 and 50% shadings started developing side branches after 65 days. Further, the number of side branches was higher in plants under 0% shading (Figure 1D).

The light available changed investment in the leaves. Although the number of leaves increased throughout the experiment, increase was more significant in plants under 0% shading after 65 days (Figure 2A). Leaf area increased during the experiment, or rather, the first evaluations registered that the leaf area was larger in higher shading treatments. However, after 80 days, there were no differences between the leaf area of plants with 0 and 70% shading (Figure 2B).

SLA decreased over time. In all evaluations, SLA was higher at 70% shading (Figure 2C). However, LAR also decreased over time. After 35, 50 and 65 days, the highest LAR was found at 70% shading and 0 and 70% shading treatments showed the highest LAR averages after 80 days (Figure 2D).

The dry matter accumulated in the root revealed small variations during the evaluation periods. There was no difference among 30, 50 and 70% shading treatments after 65 days, corresponding to higher RMR (Figure 3A). SMR remained constant in all evaluation periods at all shading levels. The highest SMR occurred after 80 days at 30 and 50% shadings (Figure 3B).

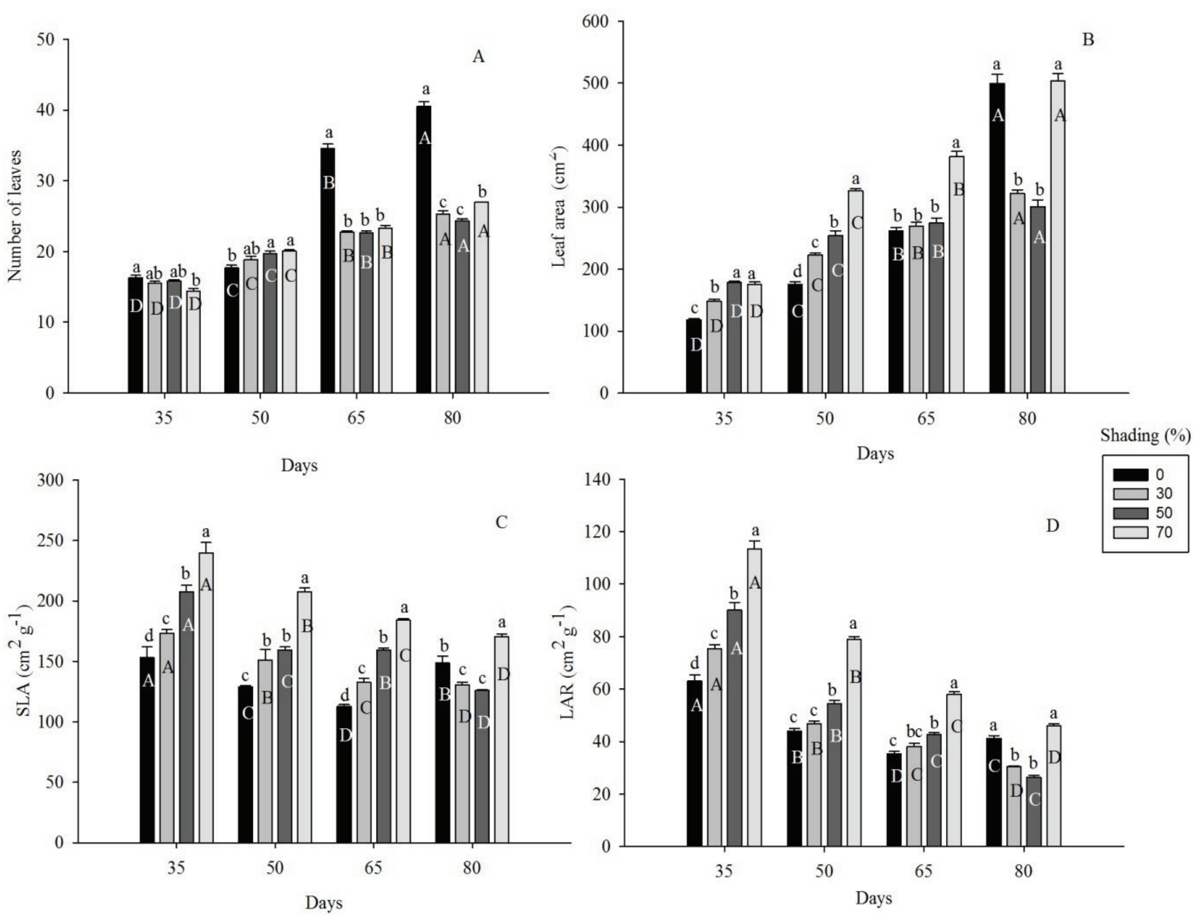

Figure 2. Number of leaves (A), leaf area (B), specific leaf area (SLA) (C) and leaf area ratio (LAR) (D) in *Cryptostegia madagascariensis* grown at four shading levels. Shades indicated by the same lower case letters did not differ for the same period; shades with the same capital letter did not differ among the evaluation periods.

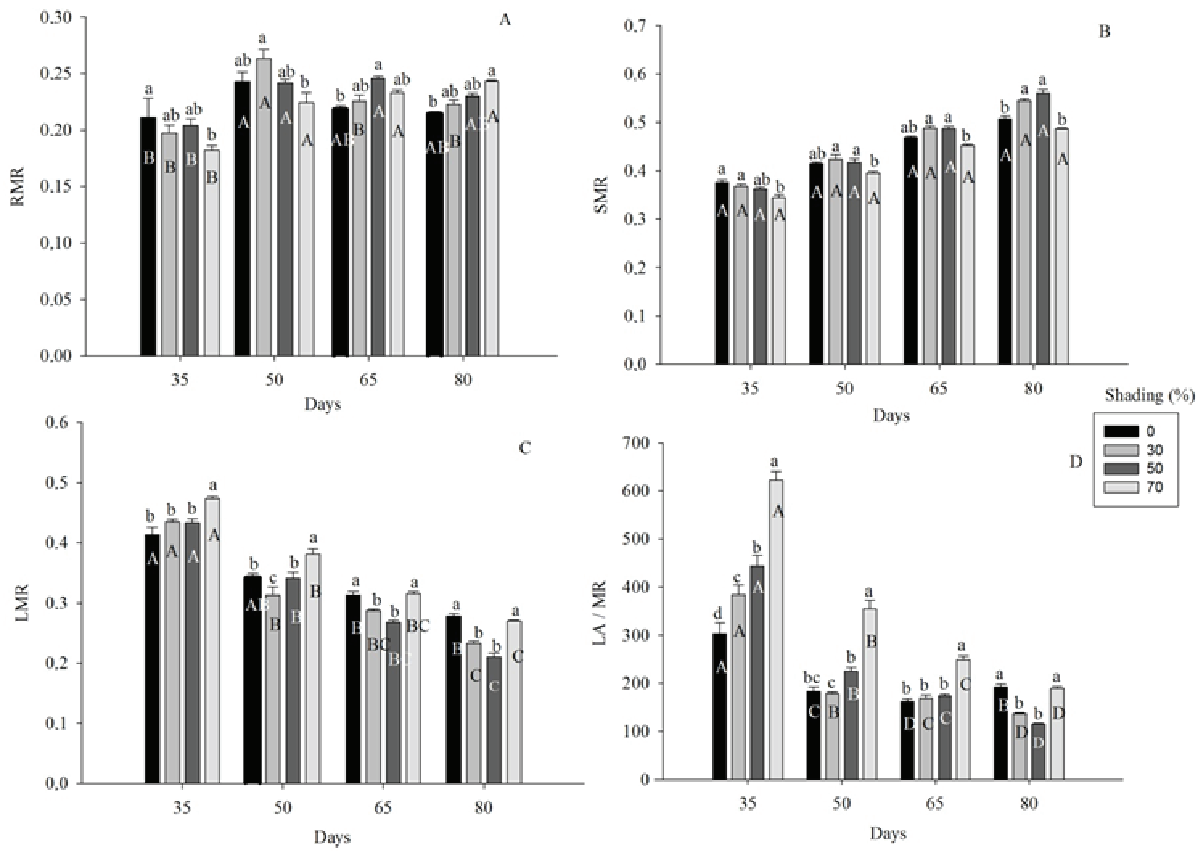

Figure 3. Root mass ratio (RMR) (A), Stem mass ratio (SMR) (B), Leaf mass ratio (LMR) (C) and leaf area/ root mass ratio (LA/RMR) (D) of *Cryptostegia madagascariensis* grown in four shading levels. Shades indicated by the same lower case letter did not differ for the same period; shades with the same capital letter did not differ among the evaluation periods.

The LMR decreased over the experiment. The highest LMR at 70% shading was reported after 35 and 50 days of treatment, whereas 0 and 70% shading treatments showed higher averages in the evaluations for 65 and 80 days (Figure 3C). The LA/MR decreased during the experiment in all shadings too. LA/MR ratio was highest at 70% shading after 35, 50 and 65 days, whereas 0 and 70% shadings had the highest averages of LA/MR after 80 days (Figure 3D).

Correlation among traits

Dry matter production in seedlings of *C. madagascariensis* under different shadings was positively related to higher leaf area ($r = 0.82$ $p < 0.01$) (Figure 4A), although it was not affected by biomass investment in the root (RMR) ($r = 0.23$) (Figure 4B). RMR increase was negatively correlated with LMR ($r = -0.62$ $p < 0.01$) (Figure 4C). Further, a negative relationship between increased height and LMR ($r = -0.87$ $p < 0.01$) (Figure 4D) was reported. In fact, RGR was determined by increasing SLA ($r = 0.63$, $p < 0.01$) (Figure 4E) and LAR ($r = 0.79$ $p < 0.01$) (Figure 4F).

Discussion

Changes in growth, investment in leaves and biomass allocation to the roots may explain the success of the initial growth of *C. madagascariensis* in environments under several variations of light availability. In fact, the success of the invasive species in different environments depends on their ability in making adjustments (DAVIS et al., 2000; FUNK, 2013). Investing in growth is a manner to escape shades (POORTER, 1999; FUNK, 2013). In fact, increase in height and AGR of *C. madagascariensis* when shaded has been registered. Greatest growth occurs in shaded plants because shade causes apical dominance (LAMBERS; POORTE, 2004), which has been observed for *C. madagascariensis* when the plant increased height and reduced the production of side branches on the reduction of available light (Figure 1A e 1D). Shaded plants had the highest stem mass ratio. This fact is highly relevant for plants that grow in these conditions because a high stem mass ratio enhances the support structure with a larger growth (QIN et al., 2012).

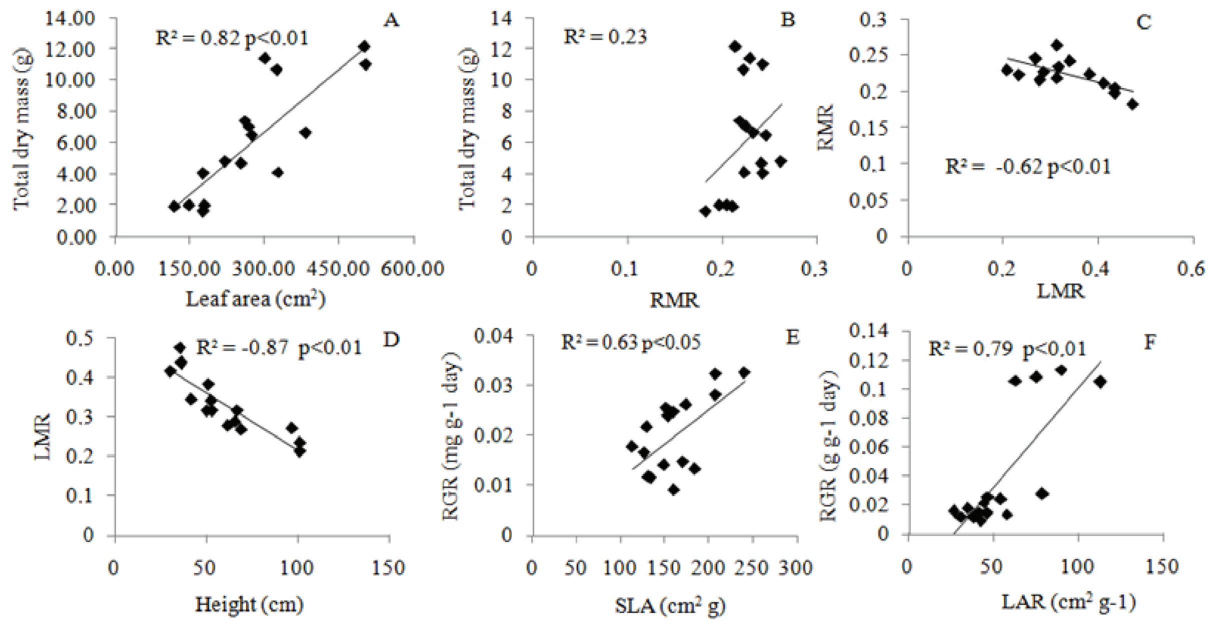

Figure 4. Correlation between leaf area and total dry mass (A), Root mass ratio (RMR) and total dry mass (B), Leaf mass ratio (LMR) and Root mass ratio (RMR) (C). Height and LMR (D), Specific leaf area (SLA) and leaf area ratio (LAR) (E), SLA and relative growth rate (RGR) (F), LAR and RGR (G) of *Cryptostegia madagascariensis* growing under different shading.

Although light is not a limiting factor in the initial growth of *C. madagascariensis* in the Brazilian semiarid, a growth variation occurs and explains why this species grows as a shrub or as a vine in invaded areas. The invasive *Vicetoxicum rossicum* also presents changes in its growth from shrub to vine. When this invasive species lies under the shade, it produces lateral branches that climb to the nearby vegetation and thus increase their competitiveness (SMITH et al., 2006). The development of lateral branches in environments under greater light availability may increase the plant's invasiveness. According to Feng et al. (2007a), it increases seed production, since the apical bud of each branch will differentiate into a floral bloom. However, the plant may adapt itself to a low and high light availability (FUNK; VITOUSEK, 2007; FUNK, 2013). Since the number of leaves increases in the plants with lateral branches, this is particularly advantageous for the plants with 0% shading due to the increase in the number of leaves and leaf area reduction per sheet. The lower leaf area reduces water loss (FAROOQ et al., 2009), without impairing the capture of light.

High leaf area in plants under shade maintains productivity, since most leaf area produces an increase in total dry matter (Figure 4A). Further, leaf area, SLA and LAR combined increase efficiency in capturing light within shaded environments (FENG et al., 2007b; ZHENG et al., 2009). The above study also reported high SLA and LAR in *C. madagascariensis* seedlings in shaded environments, which is a result of increased leaf area in the treatments. LAR decreased during the experiment, with greater efficiency in dry matter production (DANTAS et al., 2009). While high SLA is important for the establishment of invasive plants under low light availability, tolerance of plants to adverse conditions is increased (ALLRED et al., 2010). SLA is also indicated as a competitive advantage, because it is generally high in invasive plants when compared to that in native species, thereby allowing the assimilation of a larger amount of carbon (BARUCH; GOLDSTEIN, 1999; QIN et al., 2012). In fact, great assimilation of carbon by high SLA and LAR increased RGR in the *C. madagascariensis* seedlings (Figure 4E-F).

RGR increase is also an important adjustment. According to Grotkopp and Rejmánek (2007), it demonstrates greater efficiency in resources uptake related to increased invasiveness (ZHENG et al., 2012) since it facilitates adaptation to different environmental conditions. Although the first evaluations of greater RGR of *C. madagascariensis* have been observed in more shaded plants, RGR was not affected by the light availability at the end of the experiment and thus revealed the efficiency of the invasive plant to use the available light. A study of invasive *Ambrosia artemisiifolia* under different light availability also demonstrated that RGR remained unchanged at 100, 50 and 30% irradiance (QIN et al., 2012).

Variations in the allocation of biomass also increased acclimatization to different light availability. Changes in RMR over time is a trade-off between efficiency in attracting water and nutrients and the use of light (FENG et al., 2007b). This difference in biomass allocation to the roots is important for the initial establishment of the invasive plant in the semiarid region, since water absorption by the plants is associated to a positive balance between the root (RMR) and sweating the surface of the sheet, or AF/MR ratio (POORTER, 1999). RMR increase did not affect the total biomass of *C. madagascariensis* (Figure 4B), although the increased resources uptake may increase productivity (ZHENG et al., 2009). Consequently, higher RMR found in shaded environments may be a strategy to increase the carbon reservoir below the ground (FENG et al., 2007b; POORTER; ROSE, 2005).

Treatment of 0% shading caused less RMR and higher LMR, since these variables were negatively correlated (Figure 4C). Higher LMR is related to an increased carbon gain by plants (FENG et al., 2007b) and to increased invasiveness in bright environments (QIN et al., 2012). The variable increased during the experiment due to increased height (Figure 4D), and may occur with the development of plants (FENG et al., 2007b). According to Zenni et al. (2014), adaptations in invasive plants are a mechanism that increase their invasiveness and evidence their ability to acclimatize, colonize and establish themselves in different environments (THEOHARIDES; DUKES, 2007).

Conclusion

The invasive plant *C. madagascariensis* modifies its growth according to light availability by investing more on height or on the formation of side branches. Furthermore, the morphological variations on leaves to increase light availability and the changes in biomass allocation between the different organs determine the success of this invasive plant during the initial growth under different shadings. Further research should be endeavored on *C. madagascariences* to evaluate its performance when competing with native species for light.

References

ALLRED, B. W.; FUHLENDORF, S. D.; MONACO, T. A.; WILL, R. E. Morphological and physiological traits in the success of the invasive plant *Lespedeza cuneata*. **Biological Invasions**, v. 12, n. 4, p. 739-749, 2010.

BARBOSA, D. C. A. Estratégias de germinação e crescimento de espécies lenhosas da caatinga com germinação rápida. In: LEAL, I. R.; TABARELLI, M.; SILVA, J. M. C. (Ed.). **Ecologia e conservação da Caatinga**. Recife: Universidade Federal de Pernambuco, 2003. p. 625-656.

BARUCH, Z.; GOLDSTEIN, G. Leaf construction cost, nutrient concentration, and net CO2 assimilation of native and invasive species in Hawaii. **Oecologia**, v. 121, n. 2, p. 183-192, 1999.

CAVALCANTE, A.; MAJOR, I. Invasion of alien plants in the Caatinga biome. **AMBIO: A Journal of the Human Environment**, v. 35 n. 3, p. 141-143, 2006.

DANTAS, B. F.; LOPES, A. P.; SILVA, F. F. S.; LÚCIO, A. A.; BATISTA, P. F.; PIRES, M. M. M. L.; ARAGÃO, C. A. Taxas de crescimento de mudas de catingueira submetidas a diferentes substratos e sombreamentos. **Revista Árvore**, v. 33, n. 3, p. 413-423, 2009.

DAVIS, M. A.; GRIME, J. P.; THOMPSON, K. Fluctuating resources in plant communities: a general theory of invisibility. **Journal of Ecology**, v. 88, n. 3, p. 528-534, 2000.

FAROOQ, M.; WAHID, A.; KOBAYASHI, N.; FUJITA, D.; BASRA, S. M. A. Plant drought stress: effects, mechanisms and management. **Agronomy for Sustainable Development**, v. 29, n. 1, p. 185-212, 2009.

FENG, Y. L.; AUGE, H.; EBELING, S. K. Invasive *Buddleja davidii* allocates more nitrogen to its photosynthetic machinery than five native woody species. **Oecologia**, v. 153, n. 3, p. 501-510, 2007a.

FENG, Y.; WANG, J.; SANG, W. Biomass allocation, morphology and photosynthesis of invasive and noninvasive exotic species grown at four irradiance levels. **Acta oecologica**, v. 31, n. 1, p. 40-47, 2007b.

FERREIRA, W. N.; ZANDAVALLI, R. B.; BEZERRA, A. M. E.; MEDEIROS FILHO, S. Crescimento inicial de *Piptadenia stipulacea* (Benth.) Ducke (Mimosaceae) e *Anadenanthera colubrina* (Vell.) Brenan var. *cebil* (Griseb.) Altshul (Mimosaceae) sob diferentes níveis de sombreamento. **Acta Botânica Brasílica**, v. 26, n. 2, p. 408-414, 2012.

FUNK, J. L.; VITOUSEK, P. M. Resource-use efficiency and plant invasion in low-resource systems. **Nature**, v. 446, n. 7139, p. 1079-1081, 2007.

FUNK, J. L. Differences in plasticity between invasive and native plants from a low resource environment. **Journal of Ecology**, v. 96, n. 6, p. 1162-1173, 2008.

FUNK, J. L.; ZACHARY, V. A. Physiological responses to short-term water and light stress in native and invasive plant species in southern California. **Biological Invasions**, v. 12, n. 6, p. 1685-1694, 2010.

FUNK, J. L. The physiology of invasive plants in low-resource environments. **Conservation Physiology**, v. 1, n. 1, p. 1-17, 2013.

GODOY, O.; VALLADARES, F.; CASTRO-DÍEZ, P. The relative importance for plant invasiveness of trait means, and their plasticity and integration in a multivariate framework. **New Phytologist**, v. 195, n. 4, p. 912-922, 2012.

GROTKOPP, E.; REJMÁNEK, M. High seedling relative growth rate and specific leaf area are traits of invasive species: phylogenetically independent contrasts of woody angiosperms. **American Journal of Botany**, v. 94, n. 4, p. 526-532, 2007.

GUREVITCH, J.; HOWARD, T. G.; ASHTON, I. W.; LEGER, E. A.; HOWE, K. M.; WOO, E.; LERDAU, M. Effects of experimental manipulation of light and nutrients on establishment of seedlings of native and invasive woody species in Long Island, NY forests. **Biological Invasions**, v. 10, n. 6, p. 821-931, 2008.

LAMBERS, H.; POORTE, H. Inherent variation in growth rate between higher plants: a search for physiological causes and ecological consequences. **Advances in Ecological Research**, v. 34, p. 283-362, 2004.

PHONGUODUME, C.; LEE, D. K.; SAWATHVONG, S.; PARK, Y. D.; HO, W. M.; COMBALICER, E. A. Effects of light intensities on growth performance, biomass allocation and chlorophyll content of five tropical deciduous seedlings in Lao PDR. **Journal of Environmental Science and Management**, v. 1, n. 1, p. 60-67, 2012.

POORTER, H.; VAN DER WERF, A. Is inherent variation in determined by LAR at low irradiance and by NAR at high irradiance? A review of herbaceous species. In: LAMBERS, H.; POORTER, H.; VAN VUUREN, M.M.I. (Ed.). **Inherent variation in plant growth**: physiological mechanisms and ecological consequences. Backhuys Publishers, 1998. p. 309-336.

POORTER, L. Growth responses of 15 rain-forest tree species to a light gradient: the relative importance of morphological and physiological traits. **Functional Ecology**, v. 13, n. 3, p. 396-410, 1999.

POORTER, L.; ROSE, S. A. Light-dependent changes in the relationship between seed mass and seedling traits: a meta-analysis for rain forest tree species. **Oecologia**, v. 142, n. 3, p. 378-387, 2005.

QIN, Z.; MAO, D. J.; QUAN, G. M.; ZHANG, J.; XIE, J. F.; ANTONIO DITOMMASO, A. Physiological and morphological responses of invasive *Ambrosia artemisiifolia* (common ragweed) to different irradiances. **Botany**, v. 90, n. 12, p. 1284-1294, 2012.

SILVA, J. L.; BARRETO, R. W.; OLINTO, L.; PEREIRA, O. L. *Pseudocercospora cryptostegiae-madagascariensis* sp. nov. On *Cryptostegia madagascariensis*, an exotic vine involved in major biological invasions in northeast Brazil. **Mycopathologia**, v. 166, n. 2, p. 87-91, 2008.

SMITH, L. L.; DITOMMASO, A.; LEHMANN, J.; GREIPSSON, S. Growth and reproductive potential of the invasive exotic vine *Vincetoxicum rossicum* in northern New York State. **Canadian Journal of Botany**, v. 84, n. 12, p. 1771-1780, 2006.

THEOHARIDES, K. A.; DUKES, J. S. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. **New Phytologist**, v. 176, n. 2, p. 256-273, 2007.

WEIDENHAMER, J. D.; CALLAWAY, R. M. Direct and indirect effects of invasive plants on soil chemistry and ecosystem function. **Journal of Chemical Ecology**, v. 36, n. 1, p. 59-69, 2010.

ZENNI, R. D.; LAMY, J. B.; LAMARQUE, L. J.; PORTE, A. J. Adaptive evolution and phenotypic plasticity during naturalization and spread of invasive species: implications for tree invasion biology. **Biological Invasions**, v. 16, n. 3, p. 635-644, 2014.

ZHENG, Y. L.; FENG, Y. L.; LEI, Y. B.; LIAO, Z. Y. Comparisons of plastic responses to irradiance and physiological traits by invasive *Eupatorium adenophorum* and its native congeners. **Journal of Plant Physiology**, v. 169, n. 9, p. 884-891, 2012.

ZHENG, Y. L.; FENG, Y. L.; LIU, W. X.; LIAO, Z. Y. Growth, biomass allocation, morphology, and photosynthesis of invasive *Eupatorium adenophorum* and its native congeners grown at four irradiances. **Plant Ecology**, v. 203, n. 2, p. 263-271, 2009.

Received on June 16, 2015.
Accepted on September 4, 2015.

License information: This is an open-access article distributed under the terms of the Creative Commons Attribution License, which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.