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Morphological plasticity of benghal dayflower under an artificial light gradient

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ABSTRACT. The purpose of this study was to evaluate the effects of light restriction on the growth of benghal dayflower (*Commelina benghalensis*). The experiment was conducted in pots under full sunlight and with 18.5, 30, 40, 50, 60 and 70% artificial light restriction treatments. Plant growth was evaluated up to 90 days after planting (DAP), and mathematical models of the major shoot length, internode length, individual area of the first leaf completely expanded, number of leaves and shoot and root dry mass weights were established depending on increasing light restriction levels. The elevation of the light gradient promoted reductions in the number of leaves and fasciculate root dry mass weight. Light restriction did not induce alterations in the plasticity of performance (alterations in total biomass accumulation) of the *C. benghalensis* plants, the stability of which was related to an integration of the expected morphological, anatomical and physiological adjustments, constituting in a strong evidence of shading tolerance.

Keywords: *Commelina benghalensis*, shading, growth.

Plasticidade morfólogica de trapoeraba em gradiente de luz artificial

RESUMO. O objetivo deste estudo foi avaliar os efeitos da restrição luminosa no crescimento de trapoeraba (*Commelina benghalensis*). O experimento foi realizado em vasos, sob luz solar total e com 18,5, 30, 40, 50, 60 e 70% de tratamentos de restrição artificiais de luz. O crescimento das plantas foi avaliado até 90 dias após o plantio (DAP), e os modelos matemáticos do comprimento do maior ramo, comprimento de internódios, área foliar individual da primeira folha totalmente expandida, número de folhas, peso de massa seca da parte aérea e das raízes foram estabelecidos de acordo o aumento dos níveis de restrição de luz. A elevação do gradiente de luz promoveu reduções no número de folhas e massa seca das raízes fasciculadas. Restrição de luz não induziu a plasticidade de desempenho (alterações no acúmulo de biomassa total) das plantas de *C. benghalensis*, esta constância foi relacionada à integração de ajustes morfológicos, anatômicos e fisiológicos prévios, constituindo-se em um forte indício de tolerância ao sombreamento.

Palavras-chave: *Commelina benghalensis*, sombreamento, crescimento.

Introduction

The plants named dayflower belong to the Commelinaceae family, genus *Commelina*, composed of approximately 205 species (JOSEPH; NAMPY, 2012). These plants have a perennial or annual herbaceous habit and a high 'reproductive elasticity' that is the result of different propagation mechanisms by means of aerial and subterraneous seeds and shoot sprouting (JOSEPH; NAMPY, 2012; SERMONS et al., 2008). Considered a weed of major worldwide importance, the dayflower infests cotton, soybean, corn and coffee fields (CULPEPPER et al., 2004; OLIVEIRA et al., 2009).

To better establish management actions, many studies have been directed to investigate the anatomical, morphological and physiological characteristics of this species in the determination of its competitive ability and susceptibility to herbicide application (MA et al., 2011; SANTOS et al., 2002).

Nisensohn et al. (2011) verified that the accumulation of biomass was a determining factor that increased the competition capacity of *C. erecta*. Although anatomical and morphological differences between *C. benghalensis* and *C. diffusa* were verified. Santos et al. (2002) confirmed that the major tolerance of *C. benghalensis* to glyphosate herbicide in comparison to *C. diffusa* was related to physiology in association with the occurrence of sparse, small starch granules in the medullar parenchyma.

One of principal factors that affect the morphology and anatomy of the *Commelina* genus is the availability of light, showing a high morphological plasticity. Several authors described that plants subjected to light restriction exhibited a predominant shoot elongation (MARTUSCELLO et al., 2009; ZANELLA et al., 2006) and have a greater leaf area (MARTUSCELLO et al., 2009; SILVA et al., 2006b). In addition, other aspects of phenotypic plasticity, such as the speed of biomass allocation and physiological pattern adjustments and the accumulation of total biomass (named "performance plasticity"), were more related to the success of adaptation to different light conditions. However, the phenotypic plasticity of tolerant plants to shading is generally minor in comparison to that observed in intolerant plants; in addition, such differences are not constant within the diverse biological levels of organization (VALLADARES; NIINEMETS, 2008). Thus, there is a complex discussion involving the phenotypic plasticity, tolerance and competitive capacity of this species (KLEUNEN et al., 2011; RICHARDS et al., 2006). Kleunen et al. (2011) verified that the high competitive capacity of invasive species under a light gradient was not related to an adaptive plasticity to shading, at least in relation to the characteristics evaluated in their study.

Detailed mathematical modeling based on a range of developmental stages evaluated under a light gradient provides an understanding of and allows the discrimination between the morphological plasticity and shading tolerance of *Commelina benghalensis*. This fact is very important as a contribution to the establishment of the foundation to support future studies regarding the competitive capacity of this species. Therefore, the present study was conducted to evaluate how an artificial light restriction affects the growth of *Commelina benghalensis* plants.

Material and methods

The trial was established in December/2010 to March/2011 in Vitória da Conquista, Bahia State (14º53'S and 40º48'W, 960 m elevation). According to the Köppen classification, the climate is Aw, a Savanna climate with periodic rainfall and a winter with little rain. The medium annual temperature oscillates approximately 23°C, and the average annual precipitation is 730 mm.

It was utilized an access of *Commelina benghalensis* constituted by 20 plants, collected at the Experimental Station of the University of Southwestern of Bahia, located in Vitória da Conquista, Bahia State. Shoot cuttings of 0.15 m length, with three or four nodes and containing two leaves, were collected from the plants. Subsequently, the bases of the cuttings were immersed in water for a week for the formation of adventitious roots. The shoots were then planted in 10 L polyethylene pots containing a substrate composed of cultivated soil and cattle manure.

The assay was conducted in six shading structures of two meters in height, four meters in width and eight meters of in, covered with a black polyethylene mesh that restricted the sunlight by 18.5, 30, 40, 50, 60 and 70%; a full sunlight treatment was included. Ten pots containing one plant per pot were maintained in each environment, and the plants were irrigated daily, keeping the soil at the field capacity.

At 30 and 45 days after planting (DAP), it was set the total number of leaves per plant. The antepenultimate internode length in the longest branch was evaluated at 60, 75 and 90 DAP, and the length of major branch was evaluated at 30, 45, 60, 75 and 90 DAP. The individual leaf area was determined, collecting the third completely expanded leaf in the major branch of each plant, at 90 days after planting. The leaves were drawn on paper sheets with knowing density, and the leaf area estimated by weighing these profiles.

After all non-destructive analyses, at 100 DAP, four plants in each treatment were separated into the aerial parts and fasciculate and adventitious roots, and these materials were dried in a forced-air oven at 65°C for 48 hours for quantification of the dry mass.

The data were subjected to an analysis of variance and analysis of regression. In all cases, the mathematical models were chosen according to the best fitting equations and confirmed by the higher coefficients of determinations, significance of the regression coefficients and a regression F test, both at a 5% level of probability. The significance of the regression coefficients was shown in the equation, with * and ** being significant at 5 and 1% levels of probability, respectively. For statistical analysis, the software Sistema de Análises Estatísticas e Genéticas, Saeg, version 9.1, was utilized (RIBEIRO JÚNIOR; MELLO, 2009).

Results and discussion

The maximum values of the branch length varied between 0.44 (30 DAP) to 1.55 m (90 DAP) for the five evaluations (Figure 1). For all of the evaluation dates, the relationship between the shading and length of the major branch and between the shading and internode length were characterized by a linear model ($p < 0.01$), and there was an enhancement of this relationship at the later stages of development, as can be noted by the angular coefficient of the linear models. Thus, the shading effect on the increase of the branch length and internode length intensified with time, indicating a high potential of shoot adaptation for this species. The growth ability is associated with an adaptation to light restriction within the environment in which the plant develops.

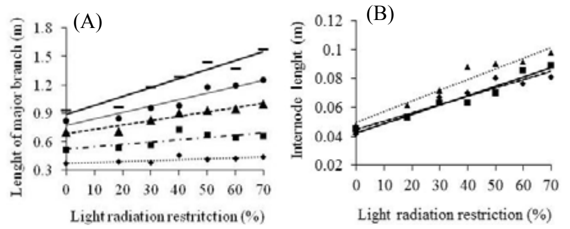

Figure 1. Length of the major branch and length of the major branch internodes. The following equations were obtained by regression analysis of benghal dayflower (*Commelina benghalensis*) subjected to different levels of artificial light restriction:(A) ♦30 days, $\hat{Y}^{*} = 0.36938 + 0.00104^{*}X$ ($r^2 = 0.6052$); ■45 days, $\hat{Y}^{*} = 0.02203 + 0.00245^{*}X$ ($r^2 = 0.5655$); ▲60 days, $\hat{Y}^{**} = 0.68139 + 0.00469^{**}X$ ($r^2 = 0.9318$); ●75 days, $\hat{Y}^{**} = 0.76933 + 0.00686^{**}X$ ($r^2 = 0.9189$); ▬90 days, $\hat{Y}^{**} = 0.88405 + 0.009465^{**}X$ ($r^2 = 0.9274$) and (B) ■60 days, $\hat{Y}^{**} = 0.044819 + 0.000576^{**}X$ ($r^2 = 0.9085$); ♦75 days, $\hat{Y}^{**} = 0.042245 + 0.000644^{**}X$ ($r^2 = 0.9483$); ▲90 days, $\hat{Y}^{**} = 0.049667 + 0.000739^{**}X$ ($r^2 = 0.9339$). *, ** $p < 0.05$ and $p < 0.01$, respectively, by the regression analysis of variance.

The slope of the branch length under the shading conditions was considered a plant strategy to maximize light harvesting. This effect was related to the plant canopy architecture resulting in an increase in the apical dominance, reducing the self-shading and causing increasing in photoassimilates (AGUILERA et al., 2004). Plant grown in sites in which the far-red radiation is abundant, in other words, under shading conditions, tend to have a longitudinal expansion (TAIZ; ZEIGER, 2009). In studies of *Passiflora edulis*, it was verified that the major length of the branch was obtained at 80% shading (ZANELLA et al., 2006). Yoshida et al. (2006) observed that the occurrence of longer and higher length of primary branches in *Commelina benghalensis* at a light restriction of 82% in comparison to plants exposed to full sunlight.

By Pearson correlation analysis, a high and positive correlation index was verified between the major branch length and internode length, 0.7378, 0.7781 and 0.8223, for 60, 75 and 90 days, respectively. Accordingly, it was deduced that the internode elongation was a determining factor to increase the major branch length. Ruberti et al. (2012) affirmed that the growth stimulation by means of elongation, which is easily verified in the internodes, is the principal response that occurs to prevent the restricting effects of a reduction of the light incidence.

A relationship between the individual leaf area and light restriction was drawn according to a polynomial model (Figure 2a). The increase in the leaf area in relation to the restriction of the light irradiation was initially characterized by a slight increase; however, this effect was accentuated with shading intensification. The major allocation of photoassimilate was directed to the shoot when the plant was subjected to shading, resulting in an elevation of the leaf area (GOBBI et al., 2011). This increase is an adaptation that enables a rapid enhancement of the photosynthetic surface and establishes the interception efficiency under shading conditions.

The reduction of the individual leaf areas of benghal dayflower at full sunlight in comparison to the shaded plants could be related to the water status. Boccalandro et al. (2009) verify that the effect of a high transpiration rate promoted by open ambient is minimized by a reduction of the leaf area through the over expression of Phy B in arabidopsis mutants. Conversely, shading-tolerant species tend to increase their leaf area under condition of lower irradiation (VALLADARES; NIINEMETS, 2008). However, Kleunen et al. (2011) indicate that this could contribute to elevate the competition capacity of a plant characterized by high shading plasticity. Increases in the competitive capacity of *C. benghalensis* were found in shaded coffee fields (higher density and frequency values) in comparison to conditions of full sun (SILVA et al., 2006a).

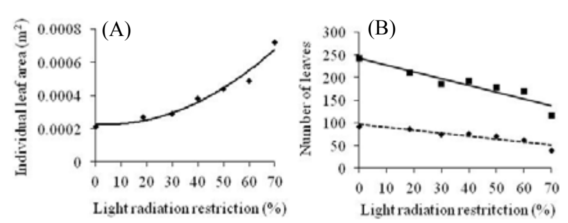

Figure 2. Individual leaf area at 90 days after planting and the total leaf number of benghal dayflower (*Commelina benghalensis*) subjected to different levels of light restriction. The following equations were obtained by regression analysis: (A) ♦$\hat{Y}^{*} = 0.000221 + 0.000008X + 0.000011X^2$ ($R^2 = 0.7727$); (B) ♦30 days, $\hat{Y}^{**} = 96.8900 - 0.6634^{**}X$ ($r^2 = 0.8587$); ■45 days, $\hat{Y}^{**} = 242.6100 - 1.4910^{**}X$ ($r^2 = 0.8734$).*, ** $p < 0.05$ and $p < 0.01$, respectively, by the regression analysis of variance.

At 30 and 45 DAP, the relationship between the total leaf number and level of light restriction was delineated by a linear model ($p < 0.05$). When compared for all of the treatments, the highest number of leaves was observed in the plants grown under full sunlight, with values rangingfrom 96 to 50 and 242 and 137 leaves at the first and second evaluations, respectively (Figure 2b).

Silva et al. (2006b) verified marked shoot etiolation, large internodal spaces and a small number of leaves in *Passiflora edulis* seedlings grown at 70% shading in comparison with plantlets maintained under full-sunlight condition.

At 100 DAP, an increasing linear effect in relation to the light restriction (LR) and shoot dry weight (SDW) was noted, with a higher value (149,87) under the 70% LR condition. A contradictory effect was observed for the total root dry mass weight (RDW), characterized by an increasing linear model, according to the increasing level of shading (Figure 3a). Higher values for the RDW were found for the full-sunlight plants, reaching a value of 59.18 g. A higher tolerance to shading was related to increasing values of the root mass weight in relation to the shoot, independent of the plasticity effect (KLEUNEN et al., 2011). In studies regarding the exposure of 46 herbaceous species to shading conditions, light restriction resulted in a greater mass allocation to the shoots than the roots (SEMCHENKO et al., 2012).

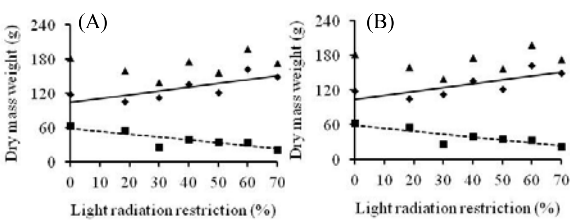

Figure 3. Total dry mass weight (TDM),shoot (SDM), total root (RDW), and fasciculate root (FRDM)and shoot adventitious root dry mass weights (SAR) of benghal dayflower plants (*Commelina benghalensis*) subjected to different levels of light radiation restriction. The following equations were obtained by regression analysis: (A) ▲TDM, $\hat{Y}$= 168.69; ♦SDM, $\hat{Y}^{*}$ = 104.0560 + 0.6545*X (r^2 = 0.5793); ■RDW, $\hat{Y}^{*}$ = 59.1818 –0.5124**X (r^2 = 0.7055); (B) ■FRDM, $\hat{Y}^{**}$ = 58.9552 – 0.5651**X (r^2 = 0.7522); ♦SAR, $\hat{Y}^{**}$ = 0.2266 + 0.0527**X (r^2 = 0.7753).*,** $p < 0.05$ and $p < 0.01$, respectively, by the regression analysis of variance.

The total dry mass weight (TDM) is an important characteristic to determine the adaptation capacity of a plant (BURNS; WINN, 2006). In the present study, the light gradient did not alter the TDM, maintaining constancy and suggesting a shading tolerance (Figure 3a). According to Burns and Winn (2006), light restriction is more effective for photoassimilate transport under shading conditions, resulting in a major accumulation of shoot mass at the expense of root development. Characteristics relative to the length of the major leaf and the higher shoot mass accumulation in comparison to the roots are important or shading tolerance (KLEUNEN et al., 2011).

It must be considered that the maintenance of biomass along a light gradient is the result of the integration of diverse anatomical, morphological and physiological alterations that occur previously in the different parts of a plant. Thus, the absence of performance plasticity (total biomass accumulation) is the result of a global process involving the occurrence of phenotypic plasticity expressed at the diverse levels of structural organization of this species.

A decreasing linear model was fit to fasciculate root dry mass weight of shoot branches (FRDM), with smaller values (19.40 g) verified at 70% LR. However, an increasing linear model was observed for the adventitious root dry mass weight, reaching maximum values (3.29 g) at 70% LR. Such alterations, when occurring simultaneously, result in an increase of the root:shoot ratio, a common phenomenon of plant tolerance to shading (VALLADARES; NIINEMETS, 2008).

Shading conditions can promote morphological alterations, such shoot etiolation, a phenomenon that enables the exploration of a more favorable niche, increasing the light-harvesting capacity. Morelli and Ruberti (2002) described that the lower ratio between the red:far-red light, characteristic of shading condition, results in a reorientation of auxin transport, which results in a major lateral transport of auxin, reducing this hormone in the roots. Thus, in the present study, there was a stimulus of adventitious root development of the shoot under the shading conditions, as can be observed by the increasing linear model that represents the relationship between the LR levels and root mass weight.

An increase in the adventitious root dry mass weight in the shoots was found when the light availability was restricted, and the quadratic effect of the shading levels to this characteristic were confirmed via a regression analysis (Figure 4). The lowest adventitious root value (1.13%) occurred when the plant was subjected to full sunlight, whereas the highest value (16.77%) was found under 70% shading. It is widely known that polar auxin transport and the establishment of an auxin gradient are very important determinants of plant growth and morphological patterning (SANTNER; ESTELLE, 2009). During root development, auxin promotes lateral root initiation, but an occurrence of any factor that compromises the expression of the auxin transporter protein PIN can reduce this effect (HONDA et al., 2011). As previously reported, the shading condition maintained the auxin level in the shoots, stimulating the pericycle to form adventitious roots at the shoot nodes.

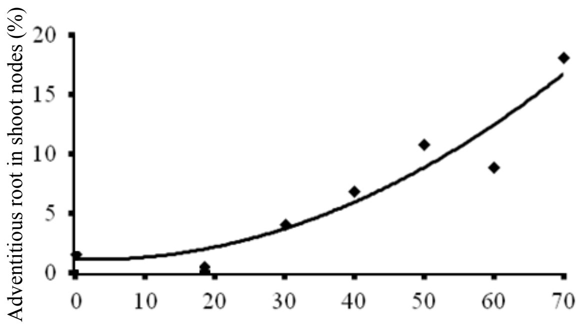

Figure 4. Percentage of the shoot adventitious root dry mass weight relative to the total root dry mass weight of benghal dayflower (*Commelina benghalensis*) subjected to different levels of artificial light restriction. The following equations were obtained by regression analysis: ♦$\hat{Y}^{**}$ = 1.12501 – 0.0163059X + 0.0034208*X^2 (R^2 = 0.9002). *, ** $p < 0.05$ and $p < 0.01$, respectively, by the regression analysis of variance.

Conclusion

Light restriction promotes the development of adventitious roots in the shoot branches and, conversely, restricts the occurrence of fasciculate roots in the principal root system. The absence of performance plasticity (biomass accumulation) is strongly indicative of a high competitive capacity of *Commelina benghalensis* in relation to the light gradient imposed in this study.

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