

Leaf anatomy and morpho-physiological mechanisms of acclimation to high irradiance in heliconia genotypes

Anatomia foliar e mecanismos morfofisiológicos de aclimação a alta irradiância em genótipos de helicônias

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ABSTRACT

The amount of solar irradiation available in the growing environment can cause significant changes in physiology and leaf anatomy that enable crops to acclimate to different light conditions. In this sense, the objective was to characterize the leaf anatomy and to elucidate the morpho-physiological mechanisms of acclimation to high solar irradiance of heliconia genotypes during the initial stage of development under semiarid conditions. The experiment was conducted in the municipality of Petrolina, Pernambuco state, Brazil (09° 19' 14" S, 40° 32' 40" W, and 387 m of altitude) and the behavior of three heliconia genotypes (*Heliconia rauliniana*; *H. bihai* cv. Lobster Claw Two, and *H. rostrata*) grown in full sun and shading (50%) environments were evaluated. At 30 days after the implementation of the experiment, leaf anatomy, chlorophyll index, plant height, number of leaves, and number of tillers were analyzed. Heliconia leaves are characterized as amphistomatous with tetracytic stomata. In its main vein there are aerenchyma structures and hypodermis on the abaxial and adaxial sides. The responses to different light conditions in plants of *H. bihai*, *H. rauliniana*, and *H. rostrata* are genotype-specific. Furthermore, the anatomical structures and physiological changes observed in *H. bihai* and *H. rauliniana* plants demonstrate that these genotypes present greater plasticity and consequently greater potential for acclimation to high solar irradiation conditions. Thus, the genotypes *H. rauliniana* and *H. bihai* emerge as a potential alternative for cultivation in gardens or in open areas and for exploration as cut flower in regions with high solar irradiation availability.

Index terms: *Heliconia* spp.; tropical flowers; luminosity; anatomical plasticity; photosynthetic pigments.

RESUMO

A quantidade de irradiação solar disponível no ambiente de cultivo pode causar alterações significativas na fisiologia e anatomia foliar que possibilite a aclimação das culturas a diferentes condições de luminosidade. Nesse sentido, objetivou-se a caracterização anatômica foliar e a elucidação dos mecanismos morfofisiológicos de aclimação a alta irradiância solar de genótipos de helicônias durante o estágio inicial de desenvolvimento em condições semiáridas. O experimento foi conduzido no município de Petrolina-Pernambuco (09°19'14" S, 40°32'40" O e 387 metros de altitude) e foram avaliados o comportamento de três genótipos de helicônias (*Heliconia rauliniana*; *H. bihai* cv. Lobster Claw Two e *H. rostrata*) cultivadas em ambientes de pleno sol e sombreamento (50%). Aos 30 dias após a implantação do experimento foi realizado análises anatômicas foliares, índice de clorofilas, altura de plantas, número de folhas e número de perfilhos. As folhas de helicônias são caracterizadas como do tipo anfiestomática com estômatos do tipo tetracítico. Em sua nervura principal há estruturas de aerênquimas e hipoderme nas faces abaxial e adaxial. As respostas as diferentes condições de luminosidade em plantas de *H. bihai*, *H. rauliniana* e *H. rostrata* são genótipo-específicas. Além disso, as estruturas anatômicas e as alterações fisiológicas observadas em plantas de *H. bihai* e *H. rauliniana* demonstram que esses genótipos apresentam maior plasticidade e consequentemente maior potencial de aclimação às condições de alta irradiação solar. Assim, os genótipos *H. rauliniana* e *H. bihai* surgem como potencial alternativa para o cultivo em jardins ou áreas abertas e para exploração como flor de corte em regiões com alta disponibilidade de irradiação solar.

Termos para indexação: *Heliconia* spp.; flores tropicais; luminosidade; plasticidade anatômica; pigmentos fotossintéticos.

INTRODUCTION

The tropical flower market has been showing constant growth and the heliconia are quite appreciated for its diversity of shapes and colors of bracts, for differentiated beauty and for presenting good resistance to transport and post-harvest duration, being exploited mainly as cut flower (Beckmann-Cavalcante et al., 2016; Gonçalves et al., 2021). Although heliconia is typical of tropical regions, studies indicate that some species when grown in high levels of light irradiation common in semi-arid regions shown drastically decreasing their growth and yield (Souza et al., 2016; Nihad et al., 2019).

The success in the production of heliconia and consequently the commercialization of the inflorescences, depends on the use of quality propagation material, the implementation of production and handlings techniques that consider the characteristics and particularities of each species, and the correct choice of species/varieties that are adapted or have potential for acclimation to the prevailing environmental conditions of the cultivation region (Souza et al., 2016; Gonçalves et al., 2021). In this way, the climatic conditions of the cultivation environment as well the availability of water and nutrients are of extreme importance for the growth and development of the plants (Santos Filho et al., 2022). However, water availability and soil nutrients are easy to control through irrigation and fertilization. In contrast, light intensity in open cultivation environment is difficult to control (Souza et al., 2016).

Light is one of the fundamental factors, that besides providing energy for photosynthesis, it also provides signals that regulate development through light receptors that are sensitive to different intensities, spectral quality, and polarization state (Durand et al., 2021). Furthermore, the amount of light or the irradiance available in the growing environment can induce significant changes in the anatomy, especially of the leaves. This mechanism is extremely important for the acclimation, growth and yield of crops (Santos et al., 2022). The leaves have a photosynthesizing role and generally present great phenotypic plasticity in relation to light radiation, of which its availability and quality influence the development, thickness, and size of the cells. However, these characteristics are dependent on genetic factors and, therefore, the potential for acclimation to light varies from species to species according to their anatomical plasticity (Earles et al., 2017; Arantes et al., 2020).

Studies of anatomy and physiology are extremely important and make it possible to understand adaptive tendencies and also the functioning of the plant in various environments (Souza et al., 2021). However, there is a

lack of studies on the behavior of heliconias, in semi-arid regions, especially in sub-medium of the São Francisco Valley, which is characterized by high incidence of solar radiation. This information is fundamental and would enable the implementation of management and the selection of superior genotypes that allow the commercial exploitation of this species as cut flowers in regions with high levels of solar irradiation. In this context, we aimed to characterize the leaf anatomy and to elucidate the morpho-physiological mechanisms of acclimation to high solar irradiance of heliconia genotypes during the initial stage of development under semi-arid conditions.

MATERIAL AND METHODS

The experiment was conducted in Petrolina, Pernambuco-Brazil (09° 19' 14" S, 40° 32' 40" W, and 387 m of altitude), in the Submédio do Vale do São Francisco. According to the Köppen classification, the region climate is BSw^h, which corresponds to a climatically arid region, with a rainy period from January to April (Alvares et al., 2013). The data on temperature, relative air humidity and solar radiation were obtained from the Davis Automatic Weather Station, model Vantage PRO 2, with temperature ($\pm 0.5\%$) and air humidity ($\pm 35\%$) sensors, located 500 m from the growing area (Figure 1).

The soil of the shaded and full sun areas were characterized as sandy loam texture, composed of 17.8 and 17 g kg⁻¹ organic matter (dry extraction method), pH (H₂O) of 6.92 and 6.06, phosphorus of 26.5 and 39.6 mg dm⁻³ of soil solution (extraction with anion exchange resin), potassium of 0.30 and 0.50 cmol_c dm⁻³, sodium of 0.11 and 0.29 cmol_c dm⁻³, boron of 0.97 and 1.15 cmol_c dm⁻³, zinc of 2.5 and 6.8 cmol_c dm⁻³ of soil (Mehlich 1 method), calcium of 2.25 and 1.64 cmol_c dm⁻³, and magnesium (KCl extraction) of 0.77 and 0.97 cmol_c dm⁻³, respectively.

Initially, heliconia seedlings were prepared through vegetative propagation via rhizomes. The rhizomes of the genotypes *H. bihai* cv. Lobster Claw Two, *H. rauliniana*, and *H. rostrata* were obtained from a commercial collection in Recife-PE (Mumbecas Farm, Guabiraba, Recife, Brazil). Rhizomes were washed, disinfected in sodium hypochlorite solution (1% active chlorine) for 20 minutes and standardized to 20 cm in length containing two buds per rhizome. Later they were grown in 20 L capacity pots filled with sand and manure in a 1:1 ratio. The material was kept under shaded conditions with 50% shading for 120 days. After this period the seedlings were standardized (one pair of expanded leaves) and transplanted to the experimental areas (full sun and 50% shading). The shading area consisted of a structure covered with 50% shade screens.

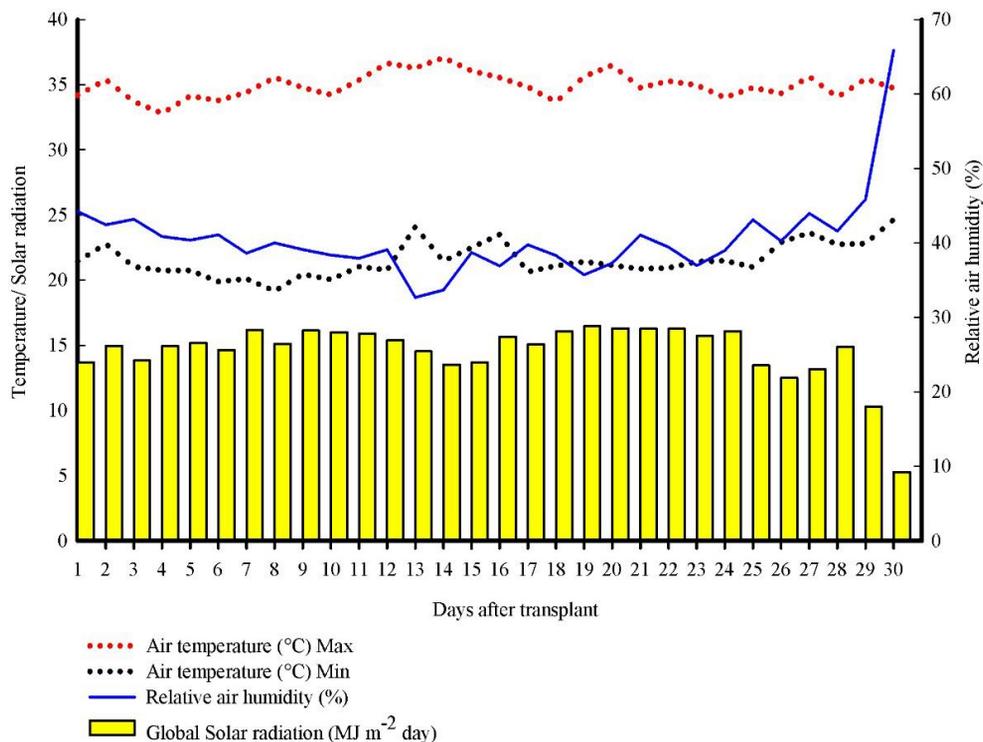


Figure 1: Air temperature (°C), relative air humidity (%), and solar radiation ($\text{MJ m}^{-2} \text{day}^{-1}$) data at the experiment site.

The transplanting of the seedlings to the experimental areas was done in 20 cm wide and 20 cm deep hole, using one seedling per hole with 1.5 plant spacing and 2.0 m between rows. At planting, 45 g of phosphorus (P) planting hole⁻¹ (Monoammonium Phosphate, 61% P_2O_5) and 2 L of tanned cattle manure were incorporated into the soil of the hole. A micro-sprinkler irrigation system was adopted with a nominal flow rate of 60 L h^{-1} and irrigation was conducted daily until field capacity was reached.

The experimental design used was completely randomized design with the treatments distributed in subdivided plots, with six repetitions (consisting per one plant). In the plots, light conditions (full sun and shading (50%) environments) were evaluated and in the subplots, heliconia genotypes (*H. rauliniana*, *H. bihai* cv. Lobster Claw Two, and *H. rostrata*).

Plant height, number of leaves, and number of tillers were evaluated 30 days after transplanting. In addition, the chlorophyll index was measured using a portable chlorophyll meter (Chlorophyll Meter, SPAD-501, Minolta Co. Japan) on two pairs of fully expanded leaves in the middle third of the plants in the morning. For the anatomical evaluations, samples of fully expanded leaves were also collected from the median portion of the plants between the

third and fifth node, for each treatment, giving preference to the central part of each plant. Then, fragments of the median portion of the leaves were submitted to fixation in FAA₇₀ solution (formaldehyde, acetic acid and 70% ethyl alcohol, in a ratio of 5:5:90 respectively) for 48 hours in vacuum and then stored in 70% ethanol (Johansen, 1940).

For structural analysis the samples ($\leq 0.125 \text{ cm}^3$) were subjected to dehydration in increasing ethyl series. After dehydration, the polymerization with hydroxyethyl methacrylate plastic resin (Leica Historessin; Heraeus Kulzer, Hanau, Germany) was performed according to Paiva, Pinho and Oliveira (2011). Cross sections of 5 μm thickness were cut with a rotary microtome (Brand: Lupe, Model: MRP-09) and subsequently stained in 0.1% toluidine blue and mounted on Entellan® (O'Brien; Feder; McCully, 1964). After making the slides, digital images were obtained with a photomicroscope (Brand: Diagtech, Model: XJD300 series) with a camera system coupled to a microcomputer and analyzed with the software Image Pro-Plus 4.0, in the region of the main vein and in the region of the second-order veins of the limbus.

The thickness of the mesophyll, palisade and spongy parenchyma, epidermis, and hypodermis on both leaf faces were measured. For surface analysis and stomata count, portions of approximately 1 cm^2 of the median portion of the

leaf were subjected to the epidermal printing technique with adhesive glue (Super Bonder®) on both epidermal faces. Stoma counts were performed on the median portion of the leaf, both on the adaxial and abaxial sides, under a light microscope in four fields. After observation of the slides, the stomatal index was calculated according to Equation 1: Where; NS is the number of stomata and EC is the number of epidermal cells.

$$\text{Stomatal Index (SI)} = \left[\frac{NS}{EC + NS} \right] \times 100 \quad (1)$$

All the data were submitted to the normality test proposed by Shapiro-Wilk and then the analysis of variance was performed with the comparison of means by the Tukey test ($p < 0.05$). All tests were performed in Sisvar software (Ferreira, 2014) and graphs were made in SigmaPlot 12.0 software.

RESULTS AND DISCUSSION

According to the variance analysis there was no effect of the growing environment (full sun and 50% shade) on the number of leaves, plant height, and number of tillers (Figure 2).

However, there was an effect of such parameters when the genotype was evaluated in isolation, where it can be seen that plants of *H. rostrata* presented the highest values of height and number of leaves when compared to *H. bihai* and *H. rauliniana* (Figure 2). The superiority in height and number of leaves in *H. rostrata* plants was expected since this species is classified as tall (Castro et al., 2011). As for the number of tillers it was observed that *H. bihai* obtained the highest values (Figure 2). The number of tillers is an extremely important characteristic in heliconia plants, since the greater the number

of tillers or shoots, the greater the number of floral stems produced and there is a strong relationship with the productive potential of the species (Souza et al., 2016). Thus, the results demonstrate that *H. bihai* plants compared to *H. rauliniana* and *H. rostrata* plants have higher yield potential.

As for the accumulation of chlorophylls, the indices of chlorophyll a (Chl a), chlorophyll b (Chl b) and total chlorophylls (Chl total) were found to be higher in *H. rauliniana* and *H. bihai* plants when grown under shaded conditions. While *H. rostrata* plants showed similar values of the chlorophyll indices (Chl a, Chl b, and Chl total) in the different light conditions (Figure 3).

This result indicates that plants of *H. rauliniana* and *H. bihai* genotype exhibit high plasticity for the accumulation of chlorophylls, investing more energy for the synthesis and accumulation of these pigments that may contribute to optimize the use of incident light and enable greater photosynthetic efficiency under shade conditions (Souza et al., 2021).

The *H. rauliniana* and *H. rostrata* genotypes showed similar behavior between full sun and shading treatments in Cha/Chlb ratio. While in plants of the *H. bihai* genotype, it was found that the light environment significantly influenced the Chla/Chlb ratio, which showed a lower ratio when grown in shading conditions (Figure 3). There was also a significant reduction in the Chl a/Chl b ratio in *H. bihai* plants, indicating increased Chl b compared to the Chl a content in the light-capturing antenna complex. This adjustment represents an important and efficient mechanism of plant adaptation to conditions of lower light intensity, since Chl b captures energy from shorter wavelengths and transfers it to Chl a, which effectively acts in the photochemical reactions of photosynthesis, increasing the quantum efficiency of photosynthesis (Lennon et al., 2021).

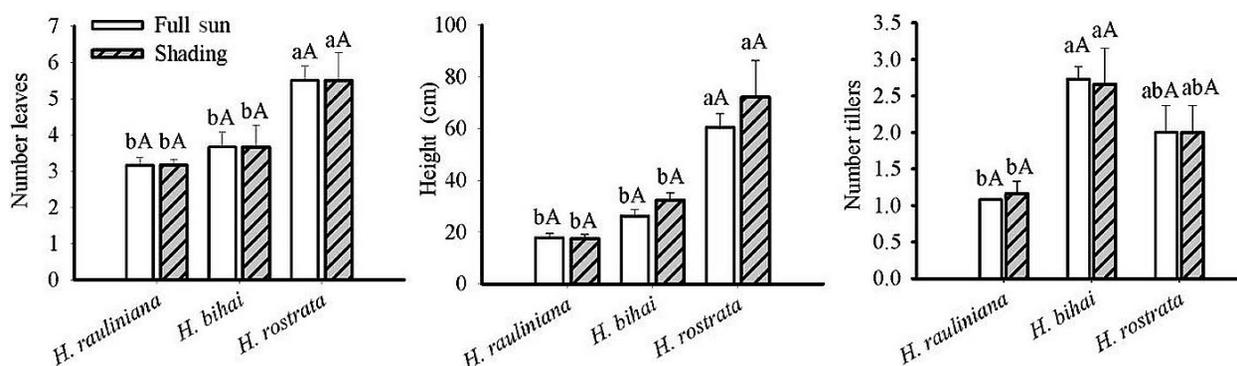


Figure 2: Leaf number, plant height, and number of tillers of heliconia (*H. rauliniana*, *H. bihai*, and *H. rostrata*) grown under full sun and shade conditions. Bars in the columns represent standard error. Averages followed by the same letter (upper case letters compare the different light conditions and lower case letters compare the genotypes) do not differ 0.05 probability using the Tukey test.

Under full sun conditions the chlorophyll content was significantly lower in *H. bihai* and *H. rauliniana* plants (Figure 3). Indicating the occurrence of a possible degradation of chlorophylls, since these pigments can be synthesized or photo-oxidized in the presence of light, and in situations of excess light, further degradation can occur and consequently decrease chlorophyll levels (Rezai et al., 2018). Additionally, this result may also reflect a better adaptation of these plants to shading conditions. Since these species are naturally from humid tropical climate conditions (Castro et al., 2011).

On the other hand, *H. rostrata* plants regardless of the lighting condition (full sun or shade) showed similar chlorophyll accumulation pattern, revealing less plasticity for this parameter (Figure 3). In this case, this lower plasticity may reduce the ability of this species to acclimate to dynamic environments.

As for the anatomical characterization, it is verified that the heliconia leaves have stomata on both sides, abaxial and adaxial, and with a predominance of stomata on the abaxial side (Figure 4). They can be classified as the amphistomatic type. In addition, the stomata of the studied species are of the tetracytic type, that is, they have four subsidiary cells, two of them parallel to the guard cells and two of them in the poles (Figure 4).

The number of stomata and the stomatal density both on the abaxial (Table 1) and adaxial (Table 2) sides showed no effect of the cultivation environment. There were differences only between the genotypes studied (Table 1 and 2). It is observed that regardless of the shade or full sun condition the leaves of *H. rostrata* plants showed higher number of stomata and index and stomatal density on both the abaxial and adaxial sides (Table 1 and 2).

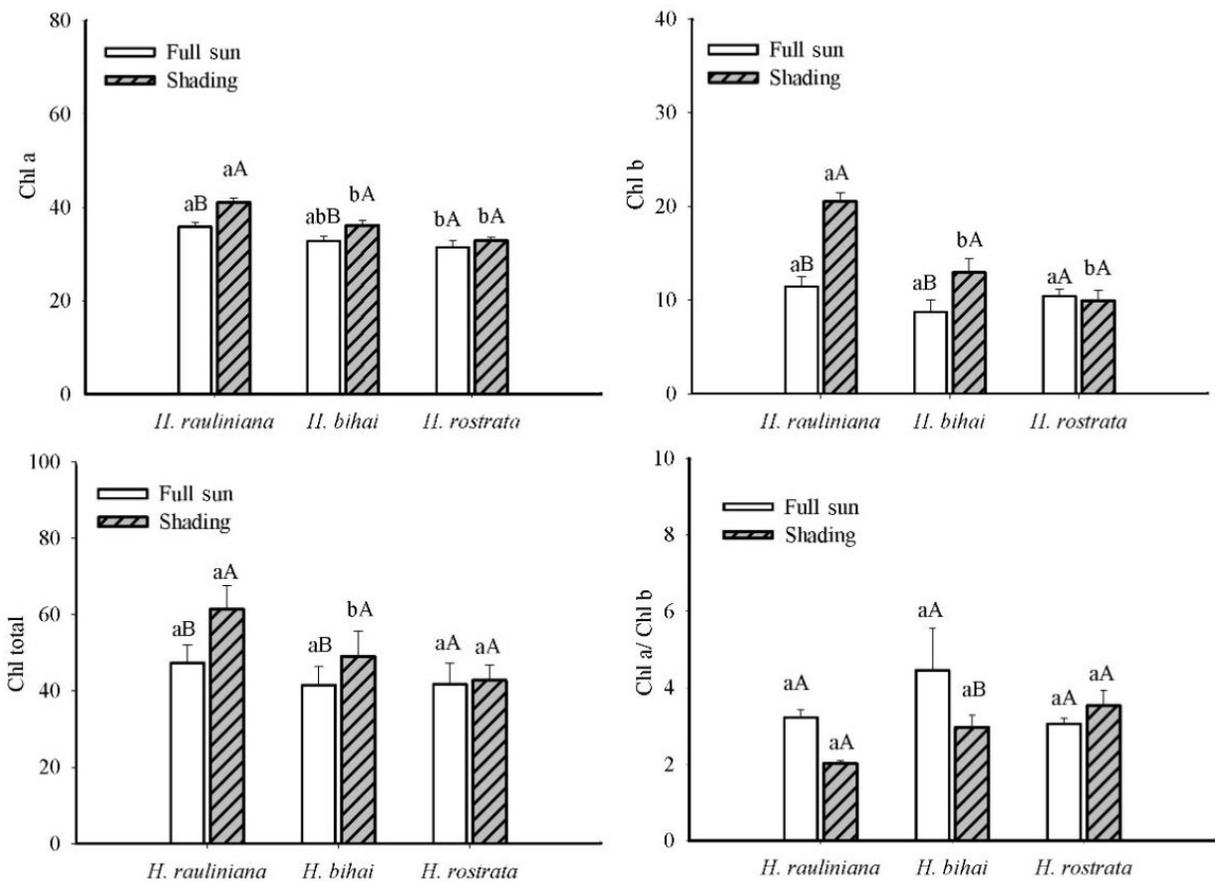


Figure 3: Chlorophyll a (Chl a), chlorophyll b (Chl b), total chlorophylls (Chl total) indices, and Chl a/Chl b ratio of heliconia (*H. rauliniana*, *H. bihai*, and *H. rostrata*) grown under full sun and shade conditions. Bars in the columns represent standard error. Averages followed by the same letter (upper case letters compare the different light conditions and lower case letters compare the genotypes) do not differ 0.05 probability using the Tukey test.

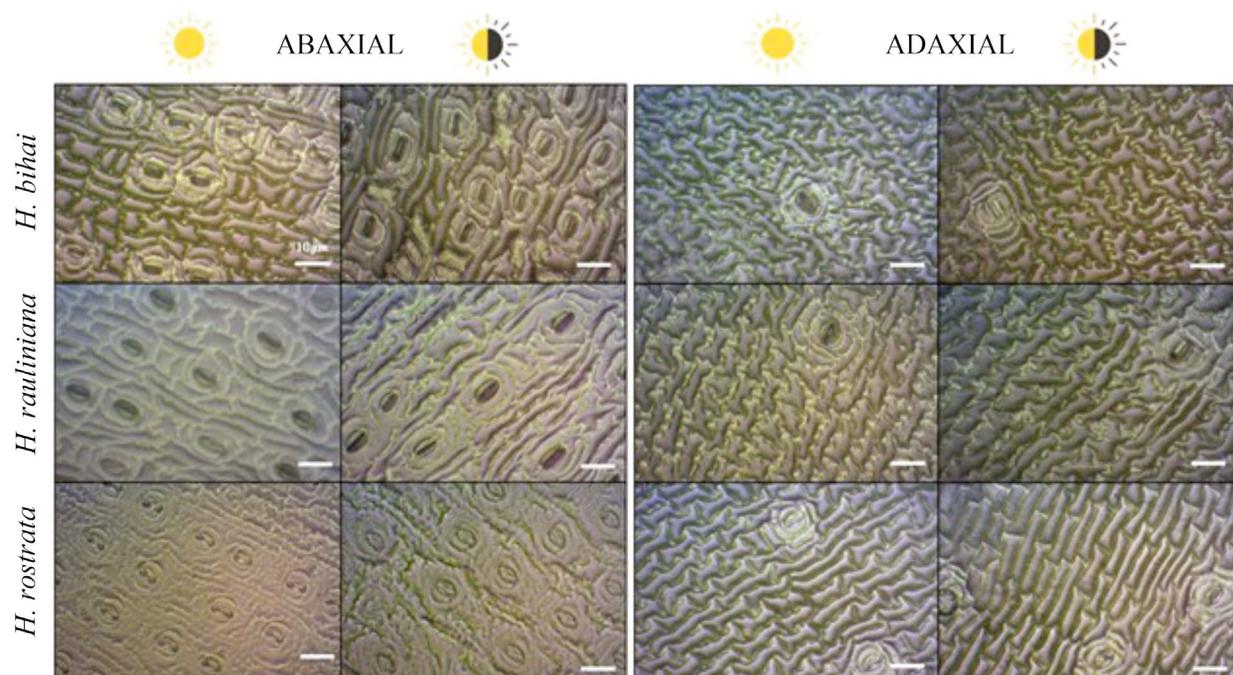


Figure 4: Epidermal printing of the epidermis on the abaxial (A) and adaxial (B) surfaces of leaves of *H. bihai*, *H. rauliniana*, and *H. rostrata* grown under full sun and shade conditions. Bars = 10 μm .

Table 1: Analysis of variance of the number of stomata (NS), number of epidermal cells (NEC), stomatal index (SI) and stomatal density (SD) of the abaxial face of heliconia plants as a function of light conditions and genotypes.

Cause of variation	NS (--)	NEC (--)	SI (%)	SD (est mm^{-2})				
F Value								
Light condition (L)	0.14 ^{ns}	0.82 ^{ns}	0.84 ^{ns}	0.13 ^{ns}				
Genotype (G)	8.58 ^{**}	2.57 ^{ns}	8.04 ^{**}	8.57 ^{**}				
Interaction L \times G	4.89 [*]	5.64 [*]	2.65 ^{ns}	4.89 ^{ns}				
C.V. (L)	12.38	24.05	55.45	12.38				
C.V. (G)	13.39	20.39	34.08	13.39				
Interaction L \times G*: "L" within each level of "G" and "G" within each level of "L"								
	Full sun	Shading	Full sun	Shading	Full sun	Shading	Full sun	Shading
<i>H. rauliniana</i>	13.0aA	10.7bA	155.2aA	150.75aA	6.66bA	7.74aA	21.27aA	25.73bA
<i>H. rostrata</i>	13.7aB	17.0aA	92.25bB	161.75aA	9.82aA	15.63aA	27.21aB	33.65aA
<i>H. bihai</i>	12.7aA	12.5bA	171.70aA	145.75aA	8.0bA	6.85aA	24.74aA	25.23bA

est = estomata; * e ** = significant at 0.05 and 0.01 probability level, respectively; ns = not significant; C.V. = coefficient of variation (%); L = Light condition; G = Genotype. Averages followed by the same letter (upper case letters compare the different light conditions and lower case letters compare the genotypes) do not differ 0.05 probability using the Tukey test.

Table 2: Analysis of variance of the number of stomata (NS), number of epidermal cells (NEC), stomatal index (SI) and stomatal density (SD) of the adaxial face of heliconia plants as a function of light conditions and genotypes.

Cause of variation	NS (--)	NEC (--)	SI (%)	SD (est mm ⁻²)				
	F Value							
Light condition (L)	0.6 ^{ns}	4.62 ^{ns}	1.02 ^{ns}	0.60 ^{ns}				
Genotype (G)	12.6 ^{**}	11.82 ^{**}	7.95 ^{**}	12.60 ^{**}				
Interaction L × G	0.6 ^{ns}	3.30 [*]	1.46 ^{ns}	0.60 ^{ns}				
C.V. (L)	35.14	6.34	38.93	35.14				
C.V. (G)	35.14	13.00	33.41	35.14				
Interaction L x G*: "L" within each level of "G" and "G" within each level of "L"								
	Full sun	Shading	Full sun	Shading	Full sun	Shading	Full sun	Shading
<i>H. rauliniana</i>	0.75 bA	1.25 bA	97.25 bA	97.00 bA	0.72 bA	1.28 aA	1.48 bA	2.47 bA
<i>H. rostrata</i>	2.23 aA	2.23 aA	127.75 aA	137.00 aA	1.73 aA	1.60 aA	4.45 aA	4.453 aA
<i>H. bihai</i>	1.23 bA	1.25 bA	140.0 aA	111.2 bB	0.86 bA	1.01 aA	2.47 bA	2.47 bA

est = estomata; * e ** = significant at 0.05 and 0.01 probability level, respectively; ns = not significant; C.V. = coefficient of variation (%); L =Light condition; G = Genotype. Averages followed by the same letter (upper case letters compare the different light conditions and lower case letters compare the genotypes) do not differ 0.05 probability using the Tukey test.

Higher stomatal density is usually associated with smaller and more easily closed stomata, and may be an anatomical adaptation that enables increased photosynthesis with high water use efficiency (Hertel et al., 2021). However, despite the higher stomatal density found in plants of *H. rostrata* it was verified that the stomata of plants of this genotype present a more spherical format compared to plants of *H. bihai* and *H. rauliniana* (Figure 4), and this format is normally associated with a lower functionality and greater difficulty in the process of stomatal closure, which may result in greater loss of water and lower potential for acclimation to semi-arid environments with predominant characteristics of high solar irradiation, low humidity and high temperatures (Souza et al., 2021).

In a transversal section of the median region of the lamina it is possible to observe that the heliconia leaves have a unistratified epidermis (a single layer of cells). In addition, the presence of subepidermal cells that are called hypodermis can be seen on both sides (Figure 5).

The palisade parenchyma of the leaves is formed by two layers, the first more compact, with more elongated cells, and the second with smaller cells. The spongy parenchyma, on the other hand, has several layers of cells of different shapes and large intercellular spaces (Figure 5). In addition, heliconia has aerenchyma structures on its main vein (Figure 6).

Aerenchyma are characterized as intercellular spaces that help decrease the weight of the leaves so that

the plant can sustain the entire leaf area. Furthermore, the presence of these structures may be constitutive in nature and reflect adaptation to humid environments and flooding (Souza et al., 2021). Since the genus Heliconiaceae occurs naturally at altitudes from sea level, in riverbanks and humid forest clearings. The hypodermis, on the other hand may have an auxiliary structural function and also store water and nutrients. Under the experimental conditions of the present study, no changes were observed in the thickness of the hypodermis as a function of luminosity (Table 3), presenting an effect only for the genotype factor, where it is observed that the leaves of *H. rostrata* plants showed lower ADH thickness than the other genotypes.

The luminosity showed an effect only on the thickness of the abaxial epidermis of the leaves, where greater thicknesses were observed in shaded conditions (Table 3). In addition, differences were also observed among the genotypes for thicknesses; of mesophyll (MES), palisading parenchyma (PP), spongy parenchyma (SP), abaxial epidermis (ABE), and adaxial hypodermis (ADH), where it is verified that the leaves of *H. rostrata* and *H. rauliniana* plants obtained the highest values (Table 3).

The hypodermis in heliconias may also be constitutive in nature and play a key role in maintaining a higher photosynthetic rate under shading conditions, due to focusing effects and reduced leaf reflectance (Karabourniotis et al., 2021). Here, we observed the presence of 2-3 layers (from

the margin to the middle of the leaf) of large hypodermis cells in the leaves of *H. bihai* and *H. rauliniana* plants under shaded conditions, while under full sun conditions these layers were reduced to 1 layer with larger cell sizes (Figure 5). This reduction in the number of layers of the hypodermis of plants grown in full sun is probably a mechanism for escaping excess light and consequently reducing the focus and reflectance of light on the leaves. On the other hand, in leaves of *H. rostrata*, the presence of 2 layers of hypodermis cells was observed both in full sun and shade conditions. Indicating a lower plasticity of this species for this trait

In the case of ABE we noticed higher values in shade conditions (Table 4), and in this case the higher ABE observed in shade plants represents an adaptation strategy to low light conditions also establishing a focusing effect, and improving the concentration of diffuse light inside the leaf. MES, PP, SP, ABE, and ADH were higher in *H. bihai* and *H. rauliniana* plants compared

to *H. rostrata* plants. According to Hertel et al. (2021) plants that have greater mesophyll, palisade and spongy parenchyma thicknesses are better adapted to sunny conditions. This higher proportion of tissues can increase the concentration and assimilation of leaf CO₂, ensuring the maintenance and efficiency of photosynthesis. It can be seen that the behavior regarding growth, chlorophyll content, and anatomical characteristics of the heliconia plants were genotype-specific. Furthermore, it can be seen that plants of *H. rostrata* showed less plasticity. Morpho-physiological plasticity, that is, the ability to vary responses and adjustments under different environmental conditions, is essential for plant adaptation to changing environments. In this sense, species that exhibit greater plasticity may be generalists in terms of environmental niches. Whereas plant species with specialized structures and with mechanisms that culminate in less plasticity may be more niche-specific (Arantes et al., 2020).

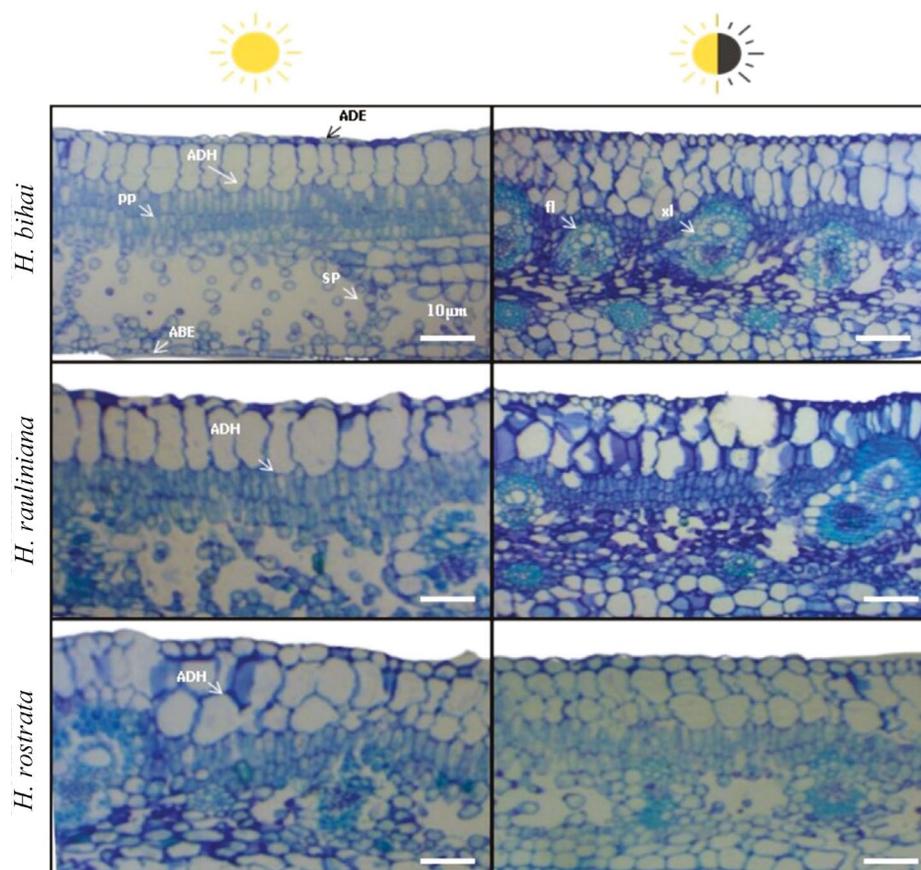


Figure 5: Leaf slides of the main vein of *H. bihai*, *H. rauliniana*, and *H. rostrata* grown in full sun and 50% shade. Bars = 10 µm. ADH = adaxial hypodermis; ABE = abaxial epidermis; ADE = adaxial epidermis; PP = palisade parenchyma; SP = spongy parenchyma; fl = phloem and xl = xylem.

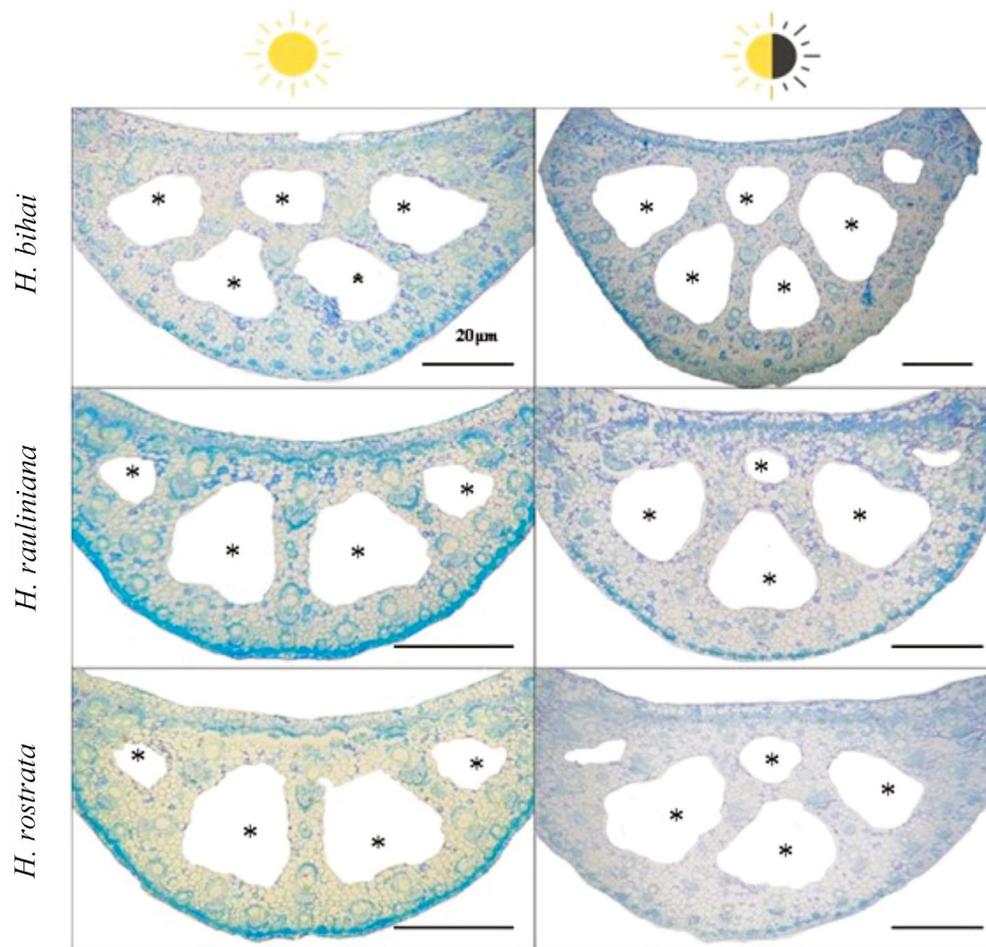


Figure 6: Leaf slides of the central vein of *H. bihai*, *H. rauliniana*, and *H. rostrata* grown in full sun and 50% shade. * = aerenchyma, Bars = 20 μm .

Table 3: Analysis of variance of mesophyll (MES), palisade parenchyma (PP), spongy parenchyma (SP), abaxial epidermis (ABE), adaxial epidermis (ADE), abaxial hypodermis (ABH), and adaxial hypodermis (ADH) thickness (μm) of heliconia plants as a function of light condition and genotypes.

Cause of variation	MES	PP	SP	ABE	ADE	ABH	ADH
	F Value						
Light conditions (L)	0.67 ^{ns}	5.14 ^{ns}	0.90 ^{ns}	11.92*	2.65 ^{ns}	7.34 ^{ns}	0.31 ^{ns}
Genotype (G)	14.62**	7.69**	9.75**	7.83**	0.38 ^{ns}	0.58 ^{ns}	9.79**
Interaction L \times G	5.87*	3.31 ^{ns}	2.95 ^{ns}	8.83**	0.82 ^{ns}	0.52 ^{ns}	6.05*
C.V. (L)	3.32	14.81	17.59	19.72	10.90	43.46	27.20
C.V. (G)	12.34	15.54	18.06	22.89	20.74	57.07	18.77

* e ** = significant at 0.05 and 0.01 probability level, respectively; ns = not significant; MSD = minimum significant difference; C.V. = coefficient of variation (%); L= Light condition; G = Genotype. Averages followed by the same letter (upper case letters compare the different light conditions and lower case letters compare the genotypes) do not differ 0.05 probability using the Tukey test.

Thus, the same leaf structure in terms of stomatal density, chlorophyll content, and anatomical structures found in *H. rostrata* plants indicates less ability to acclimate to different environmental conditions. Furthermore, the results indicate that the high irradiance available in the short-term (30 days) full sun environment does not alter the leaf structure of *H. rostrata* and may compromise the process of acclimation to high irradiance conditions. Once, the induction of adjustments and rapid mechanisms of morphoanatomical and physiological responses during the process of acclimatization to different environmental conditions is essential to ensure the adaptation and survival of plants to dynamic and stressful environmental conditions (Souza et al., 2021). In contrast, the genotypes *H. rauliniana* and *H. bihai* show high morpho-physiological plasticity and consequently a greater potential for acclimation to full sun cultivation in regions with the availability of high solar irradiance.

H. rostrata is a genotype highly appreciated as a cut flower and has a high market value compared to the *H. bihai* and *H. rauliniana* genotypes, however, our results demonstrate that its cultivation in regions with availability of high solar irradiance should be restricted to shaded environments. On the other hand, the *H. rauliniana* and *H. bihai* showed greater ability to acclimation to conditions of high levels of irradiance, being an excellent alternative for cultivation in gardens or in open areas in full sun and also for exploration as cut flowers in regions with high availability of solar radiation.

CONCLUSIONS

The responses to different light conditions are genotype-specific. Furthermore, the anatomical structures and physiological changes observed in *H. bihai* and *H. rauliniana* plants demonstrate that these genotypes have greater plasticity and consequently greater potential for acclimation to high solar irradiance conditions. Thus, the genotypes *H. rauliniana* and *H. bihai* emerge as a potential alternative for cultivation in gardens or in open areas and also for exploration as cut flowers in regions with high solar irradiation availability.

AUTHORS CONTRIBUTION

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REFERENCES

- ALVARES, C. A. et al. Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift*, 22(6):711-728, 2013.
- ARANTES, M. K. et al. Phenotypic plasticity of leaf anatomical traits helps to explain gas-exchange response to water shortage in grasses of different photosynthetic types. *Theoretical and Experimental Plant Physiology*, 32(2):341-356, 2020.
- BECKMANN-CAVALCANTE, M. Z. et al. Nitrogen and potassium fertilization in yield and macronutrients contents of heliconia cv. Golden Torch. *Revista Brasileira de Engenharia Agrícola e Ambiental*, 20(4):337-342, 2016.
- CASTRO, C. E. et al. Helicônias brasileiras: Características, ocorrência e usos. *Revista Brasileira de Horticultura Ornamental*, 17(1):5-24, 2011.
- DURAND, M. et al. Diffuse solar radiation and canopy photosynthesis in a changing environment. *Agricultural and Forest Meteorology*, 311:108684, 2021.
- EARLES, J. M. et al. Excess diffuse light absorption in upper mesophyll limits CO₂ drawdown and depresses photosynthesis. *Plant Physiology*, 174(2):1082-1096, 2017.
- FERREIRA, D. F. Sisvar: A guide for its bootstrap procedures in multiple comparisons. *Ciência e Agrotecnologia*, 38(2):109-112, 2014.
- GONÇALVES, C. et al. Heliconias with pendent inflorescences as cut flowers. *Ornamental Horticulture*, 27(2):137-154, 2021.
- HERTEL, M. F. et al. Different leaf traits provide light-acclimation responses in two neotropical woody species. *Theoretical and Experimental Plant Physiology*, 33(2):313-327, 2021.
- JOHANSEN, D. A. *Plant microtechnique*. New York: McGraw-Hill Book Co. Inc., 1940. 423p.
- KARABOURNIOTIS, G. et al. The optical properties of leaf structural elements and their contribution to photosynthetic performance and photoprotection. *Plants*, 10(7):1455, 2021.
- LENNON, A. M. et al. Photochemical responses to light in sun and shade leaves of *Theobroma cacao* L. (West African Amelonado). *Scientia Horticulturae*, 276:109747, 2021.

- NIHAD, K. et al. Photochemical and biochemical responses of heliconia (*Heliconia stricta* "Iris") to different light intensities in a humid coastal environment. Horticulture, Environment, and Biotechnology, 60(1):799-808, 2019.
- O'BRIEN, T. P.; FEDER, N.; McCULLY, M. E. Polychromatic staining of plant cell walls by toluidine blue O. Protoplasm, 59:368-373, 1964.
- PAIVA, E. A. S.; PINHO, S. Z.; OLIVEIRA, D. M. T. Large plant samples: how to process for GMA embedding? In: CHIARINI-GARCIA, H.; MELO, R. C. N. (Eds.) Light microscopy methods in molecular biology. Humana Press, Totowa, NJ, v.689, p.37-49, 2011.
- REZAI, S. et al. Effect of light intensity on leaf morphology, photosynthetic capacity, and chlorophyll content in sage (*Salvia officinalis* L.). Horticultural Science and Technology, 36(1):46-57, 2018.
- SANTOS FILHO, F. B. et al. Polyamines mitigate the harmful effects of salt stress on the growth and gas exchange of nasturtium. Ciência e Agrotecnologia, 46:e000722, 2022.
- SANTOS, J. W. G. et al. Quantitative and qualitative responses of *Euphorbia milii* and *Zamioculcas zamiifolia* exposed to different levels of salinity and luminosity. Revista Ciência Agronômica, 53:e20218070, 2022.
- SOUZA, R. R. et al. Morpho-anatomical changes and antioxidant enzyme activity during the acclimatization of *Genipa americana*. Acta Physiologiae Plantarum, 43:93, 2021.
- SOUZA, R. R. et al. Yield and quality of inflorescences of 'Golden Torch' heliconia in different shaded environments. Revista Brasileira de Engenharia Agrícola e Ambiental, 20(2):128-132, 2016.