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# Ecophysiology and production of red pitaya under different light conditions

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**Abstract**

In commercial orchards of red pitaya fruit, yellowish cladodes frequently occur, mainly in the warmest months of the year. The measurement of probable interferences on the ecophysiology and production of red pitaya and their correlations are unprecedented and may present a basis for commercial producers. This study aimed to analyze the effect of different light conditions on growth, anatomy, photosynthetic pigments, gas exchanges, and the production of red pitaya in Fortaleza (CE).
The experimental design was carried out in randomized blocks (RDB), with five treatments, five replications, and two plants per plot. The treatments consisted of five levels of luminosity: full sunlight, 35, 50, 65, and 80% shading, with the use of PVC shade screens. At 365 days, morphological, biochemical, physiological, and anatomical characters were analyzed. The fruit production was estimated from the first fruit emission, which occurred 186 days after the experiment installation. It is concluded that the luminosity conditions interfere with a variably in the growth, anatomical structures, photosynthetic pigments, gas exchanges, and production, as well as on their correlations. The crop presented high phenotypic plasticity and adequately acclimated to cultivation in full sunlight, obtaining the highest production. Moreover, this study recommended cultivating in full sunlight and at 35% shading, which showed the greatest performances in terms of ecophysiological variables and productive yield.

**Keywords:** Anatomy, *Cactaceae*, Exotic fruits, Hylocereus costaricensis, Shading.

**Introduction**

Red pitaya (*Hylocereus costaricensis*) is a semi-epiphytic, perennial, succulent cactaceous plant with cladode (as stem), which generates numerous adventitious roots for attachment to tutors. The flower is a hermaphrodite, white, large in size, and nocturnal anthesis. The reddish skin and pulp, pleasant taste, slightly sweet make this fruit very attractive to consumers (Cajazeira et al., 2018; Marques et al., 2011).
The genus *Hylocereus* contains 14 species, found in subtropical and tropical forest regions of the American continent. Among the *Hylocereus* species cultivated worldwide, it is highlighted the *H. undatus*, *H. costaricensis*, *H. polyrhizus*, H. *monacanthus* and *H. megalanthus.* Red pitaya is found especially in Costa Rica, El Salvador, Guatemala, and Mexico. Although, the prices charged worldwide have been incited the expansion and intensification of this culture into different planting systems in countries such as Mexico, Nicaragua, Malaysia, Vietnam, Israel, and Brazil. The red pitaya cultivated in Brazil occurs predominantly in small crops, and due to the price, its commercialization is restricted to markets with higher purchasing power (Ortiz-Hernández and Carrillo-Salazar, 2012). Red pitaya is an exotic species in Brazil. In other words, it was introduced by human action, either accidentally or intentionally. Red pitaya has good acceptance for fresh consumption due to its sensory characteristics and exotic visual aspect. The cultivation of red pitaya in Brazil is recent, having started around 15 years ago in São Paulo state. Posteriorly, commercial crops were implanted in the state of São Paulo, Minas Gerais, Paraná, Santa Catarina, Mato Grosso do Sul, Rio Grande do Norte, Ceará, and Pernambuco (Silva, 2014). In Ceará State, the production is concentrated in the Apodi Plateau (Chapada do Apodi), more precisely in the municipalities of Limoeiro do Norte and Quixeré. The average productivity ranges from 10 to 30 t $ha^{-1}$, depending on soil and climatic conditions, cultivation techniques, and orchard age. Concerning environmental factors, sunlight works in the regulation of several plant development processes, such as photosynthesis and pigment biosynthesis (Almeida et al., 2016a; Nunes et al., 2014). The red pitaya, under natural conditions, is found in the shaded rainforest understories of America, which suggests that when cultivated commercially, it is necessary to install structures to provide artificial shading to the crop.

In this context, several studies were conducted over the world, such as in Israel (Mizrahi and Nerd, 1999; Mizrahi, 2014) and also in Brazil (Cavalcante et al., 2011), attesting to the need for shading taking into consideration the local climate and the phenological stage of the culture. Nevertheless, Mizrahi (2014) claimed in their study that some species of the genus *Hylocereus* could be tolerant to sunlight since this species present thicker wax layers in the extension of the cladodes, avoiding, thus, direct exposure of the stomata to solar radiation.

In the state of Ceará, the orchards are cultivated in full sunlight; it is evidenced by the occurrence of plants with yellowish cladodes, particularly in the warmest months of the year. The measurement of changes in the growth, ecophysiology, and production of red pitaya, as well as their correlations, is still incipient in the scientific literature; it is worth mentioning that these pieces of information are relevant and could provide a data basis for researchers and commercial producers.

Based on the above considerations, this study aimed to analyze the effect of sunlight intensity on the morphological, biochemical, physiological, anatomical, and productive characteristics of red pitaya in the edaphoclimatic conditions of Fortaleza (Ceará state).

**Results and discussion**

***Effect of different light conditions on growth***

The results obtained in this study demonstrated that the treatments had a significant effect ($p < 0.05$) on all morphological characters analyzed. The sum of the length of lateral sprouts (SLLS) increased linearly, according to the increment of artificial shading (Figure 1A).

At 80% shading, the sum of the length of lateral sprouts (23.60%) was greater than the control (full sunlight) by the linear regression model (Figure 1A). This result was as expected, being in line with studies of Andrade et al. (2006) and Cavalcante et al. (2011), who also found elongated cladodes under conditions of 50 and 80% shade, respectively. Plants that were grown under 80% shading also showed a higher number of lateral sprouts (NLS) and evidenced an increase in vegetative growth both by elongating cladodes (SLLS) and by branches (NLS) (Figures 1A and 1B).

Terminal sprout diameter (TSD) reduced linearly as the reduction in luminosity in the growing environment (Figure 1C). The largest diameter was estimated in full sunlight, and possibly it was a result of the plants acclimating to this light condition. For the arch thickness (TSAT), a situation similar to the TSD was evidenced, up to 35% shading, after a reduction in the TSAT values (Figure 1D) were observed.

In this context, by associating the diameter, thickness, and the sum of the length of the sprouts (Figures 1A, 1C, 1D), it was noticed that plants grown in full sunlight had smaller and thicker cladodes, whereas, under 80% of shading, the opposite was evident, elongated and thin cladodes.

As the morphology of cladodes on 80% shading is in accordance with the description of Merten (2003) for etiolated cactus; therefore, the etiolation was expected to occur at 80% shading. In order to provide a more solid scientific basis for the explanation of this hypothesis, biochemical, physiological, anatomical, and production analysis of the red pitaya tree were carried out.

Figure 2 shows the anatomical characteristics of red pitaya cladodes, in full sunlight (2A, 2B, and 2C), and 80% shading (2D, 2E, and 2F).

It must be evidenced that even though red pitaya is a semi-epiphyte cactus (Almeida et al., 2016c), it may be considered xeromorphism due to its anatomical characteristics (epidermis covered by a thick cuticle, collenchymatic hypodermis, aquifer parenchyma, mucilage secreting structures, among others) and morphophysiological characteristics (succulent cladodes, presence of spines, and nocturnal carbon fixation (CAM metabolism), among others). Xeromorphism consists of typical adaptations of Cactaceae, reported in botanical studies, such as those by Aguilar et al. (2013). The presence of mucilage-secreting structures, irregularly distributed in the parenchyma, was a common characteristic detected in all sections of cladodes analyzed in full sunlight and 80% shading (Figure 2). According to Arruda and Melo-de-Pina (2015), this is related to water storage in cladodes, which may be favorable to the acclimatization and production of this species in non-shaded environments.

Among the anatomical sections collected in cladodes of plants grown in full sunlight and 80% shading, only the cross-section on the abaxial face provided a comparison between cuticle thickness and epidermis-hypodermis. However, for other treatments, as a characterization method of red pitaya grown on different luminosity levels, the averages with the standard error were presented, and anatomical structures were identified.

The thickness of the cuticle (CT) and the epidermis-hypodermis (EHT), obtained from the cross-section, abaxial, and full sunlight, and transversal, abaxial, at 80% shading, presented a significant effect ($p < 0.01$) for the luminosity intensity. The variation coefficients were estimated at 15.59 and 4.01%, respectively, and indicated good experimental precision.

For cultivation in full sunlight, the section presented a cuticle thickness (CT) of 14.18 µm, whereas, under 80% shading, the average was 5.68 µm (Table 1, Figure 2). This drastic anatomical difference can be related to the greater solar radiation at full sunlight, which stimulates the expression of photoprotection mechanisms by the culture.

According to Aguilar et al. (2009), the presence of a thickness cuticle in cactus and other groups of xerophytic plants reduces the water losses through transpiration and helps the epidermis in the protection of photosynthetic tissues. In this sense, the increase in cuticle thickness at full sunlight may have worked as a physical barrier to solar radiation and water losses.

The range from 5.68 to 14.18 µm was similar to the cuticle thickness obtained by Boeger et al. (2010) in cactus. According to the classification presented by Dettke and Milaneze-Gutierre (2008), these results can be characterized as "thick cuticle" and "moderately thick cuticle" for cultivation at full sunlight and 80% shading, respectively.

About the epidermis-hypodermis thickness (EHT), the highest average was obtained under 80% shading and revealed that in low luminosity conditions, there was an increase of 7.34% (13.38 µm) in the thickening of the tissue (epidermis-hypodermis) (Table 1). The means of EHT confirm those results found by Aguilar et al. (2009) for three species of the genus *Hylocereus* (*H. ocamponis, H. purpusii,* and *H.* undatus). Probably, the reduction in EC and the increase in EHT, at 80% shading, were purposed to increase the efficiency of capturing light where solar radiation was a scarce factor. For cross-section, adaxial face, and longitudinal section, abaxial face, at 80% shading, cuticle thicknesses of 8.97 ± 1.32, and 8.74 ± 0.69 µm were obtained, respectively (Table 2). These values corroborate those presented by Dettke and Milaneze-Gutierre (2008). According to the classification of these authors, the cuticles for these sections can be classified as "moderately thick" and have characteristics similar to those seen in Figures 2D and 2E.

In turn, the values found for the thickness of the epidermis-hypodermis of the cross-section, adaxial face, full sunlight and longitudinal section, abaxial face, at 80% shading, were 139.01 ± 3.14 and 141.92 ± 5.53 µm, respectively (Table 2). According to Rosas et al. (2012), the presence of hypodermis in the cactus is important, as the cell walls of this tissue hold high concentrations of hemicellulose and pectin, which contribute to water-storage on cladodes. The anatomical characteristics were shown in Figures 2A, 2B, 2D, and 2E.

***Effect of different light conditions on photosynthetic pigments***

Regarding the accumulation of photosynthetic pigments, it was observed that there was a significant effect ($p$ <0.05) of the treatments on the levels of chlorophyll-*a* (chlor *a*), chlorophyll-*b* (chlor *b*), total chlorophyll (chlor *t*), and carotenoids (caroten). The variation coefficients ranged from 8.14 to 14.16% and indicated good experimental precision.

At full sunlight, the lowest average levels of chlorophyll *a*, *b,* and total (*t*) were determined; these results may be associated with the abundant luminosity in the cultivation area, considering that in shading conditions, the opposite occurred (Figures 3A, 3B, and 3C). These results corroborate with Souza et al. (2011), who noticed that for the shaded plants, there is a greater accumulation of total chlorophyll than in those grown in full sunlight. It possibly occurred to increase the efficiency of light capture under low solar radiation. The results obtained in this study demonstrated that the treatments had a significant effect (p <0.05) on all morphological characters analyzed. The sum of the length of lateral sprouts (SLLS) increased linearly, according to the increment of artificial shading (Figure 1A). These results corroborate with Souza et al. (2011), who noticed that f shaded plants, there is a greater accumulation of total chlorophyll than in those grown in full sunlight. It possibly occurred to increase the efficiency of light capture under low solar radiation. The carotenoids accumulation demonstrated the opposite behavior to that seen for total chlorophyll. The highest average was obtained in full sunlight and helped to understand the yellowish color in the extension of cladodes under this light condition (Figure 3D). Perhaps, the greatest accumulation of carotenoids in full sunlight was a photoprotection mechanism of red pitaya. This hypothesis was in line with the study of Barbosa-Campos et al. (2018) and Li et al. (2014), who explained that carotenoids are pigments with a photo-protective function and act by rapidly extinguishing the excited states of chlorophyll, protecting it from photo-oxidation, in environments with intense solar radiation. Plants that grew into 65 and 80% shading showed similar levels of total chlorophyll, which were superior to other light conditions being in accordance with Voltolino et al. (2011), who reported higher accumulations for shading plants when compared to cultivation in full sunlight.

***Effect of different light conditions on gas exchange and fruiting***

About the gas exchange characters, significant effects (p <0.05) of the light intensity on the net carbon assimilation, stomatal conductance, transpiration, $C_i/C_a$ ratio, instant water use efficiency, and efficiency carboxylation were noticed. The variation coefficients ranged from 2.93 to 20.45% and indicate good experimental precision for field conditions.

The net assimilation of carbon (*A*) ranged from 8.21 to 13.41 mmol $m^{-2}$ $s^{-1}$, with the best yields obtained in full sun and 35% shading, which did not differ statistically (Figure 4A).

Regardless of in full sunlight, the plants presented slight vegetative growth (Figure 1) and accumulation of total chlorophyll (Figure 3); the red pitaya showed good net carbon assimilation compared to shading treatment, particularly with 35%.

A higher accumulation of carotenoids in the extension of the cladodes may have favored the damage reduction on photosynthetic apparatus and allowed greater photosynthetic efficiency in full sunlight, although the culture is considered as semi-epiphytic *Cactaceae*. In this sense, it is important to stand out the transpiration (BE) obtained in full sunlight, as well as its relationship with gs and C*i* (Figure 4B, 4C, and 4D). In this condition, there was also a higher C*i*/C*a* ratio, carboxylation efficiency (*A*/C*i*), and instant water use efficiency (*A*/*E*) (Figure 5A, 5B, and 5C).

It is worth highlighting the good productive ability of photoassimilates (A) with fewer water losses, compared to shading treatments. In other words, in a morphophysiological analysis, cactus already have efficient water use mechanisms. However, in the case of red pitaya, under certain cultivation conditions, there was a greater expression of this acclimatization, principally at full sunlight cultivation. In this context, until the 365 days of evaluation, the best fruit production was obtained at full sunlight (Figure 6). These results were opposed to the range of 30 and 60% of shading, recommended by Cavalcante et al. (2011), Nobel and De La Barrera (2004), and Mizrahi (2014), for crops of *Hylocereus* sp. Therefore, the adoption of the shade structure used to cause gradual reductions in the solar radiation available to plants was not adequate to increase the production of red pitaya, up to 365 days, in the present study. Thus, further research must be conducted in order to show the tendency of greater fruiting in full sunlight so that this treatment can be properly recommended for the commercial cultivation of red pitaya in Fortaleza (Ceará state) and other cities with similar edaphoclimatic conditions. Almeida et al. (2018) noticed positive effects of 35% shading on growth and gas exchanges of red pitaya up to 180 days. In the present research, quite similar results were obtained in growth exposed to full sunlight. Therefore, most extensive studies may emphasize the viability of additional costs for the implementation of shading structures given the productivity and useful life of perennial orchards cultivated in full sunlight. About the correlations between the growth characters, gas exchange, and fruit production, the results showed that at full sunlight, there were correlations from medium to the high magnitude of fruit production with transpiration (E), instantaneous water use efficiency (*A*/*E*), and the number of lateral sprouts (NLS) (Table 3).

**Table 1.** Comparison of means referring to cuticle thickness (CT) and epidermis-hypodermis (EHT) in anatomical sections of red python cladodes, grown under different light conditions.

| Treatment | CT (µm) | EHT (µm) |
|---|---|---|
| Cross section, abaxial face, full sunlight | 14.18 a | 168.98 b |
| Cross section, abaxial face, 80% shading | 5.68 b | 182.36 a |
| Msd | 0.80 | 3.64 |
| CV (%) | 15.59 | 4.01 |

Means followed by the same letter, in the column, do not differ by Tukey's test; msd = minimum significant difference; CV = Coefficient of variation.

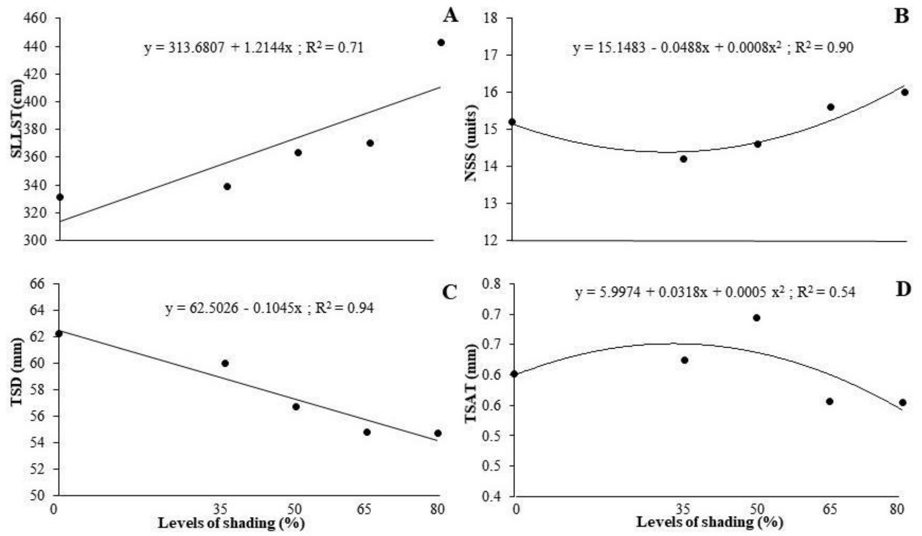


**Figure 1.** Effect of shading on the growth of red pitaya, at 365 days after the installation of the experiment. **1A:** sum of the length of lateral sprouts (SLLS); **1B:** number of lateral sprouts (NSLS); **1C:** terminal shoot diameter (TSD); **1D:** terminal shoot arch thickness (TSAT).

**Table 2.** Characterization of cuticle thickness (CT) and epidermis-hypodermis (EHT), in anatomical sections of red python cladodes, grown under 80% shading.

| Treatment | CT (µm) | EHT (µm) |
|---|---|---|
| Cross section, adaxial face, 80% shading | 8.97 ± 1.32 | 139.01 ± 3.14 |
| Longitudinal section, abaxial face, 80% shading | 8.74 ± 0.69 | 141.92 ± 5.53 |

The data represent the mean ± the standard error, in 30 samples (n = 30).

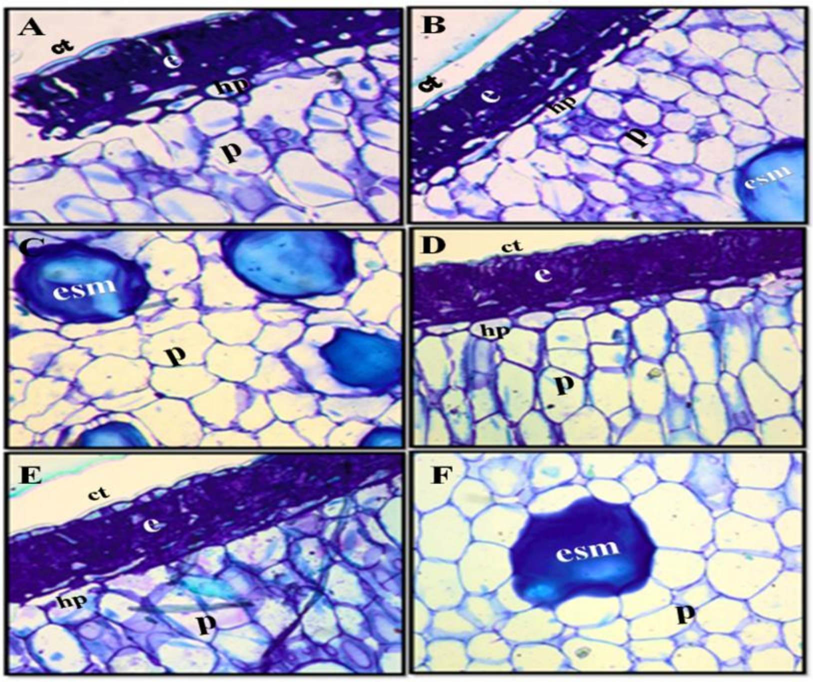


**Figure 2.** Cross sections of the abaxial face of red pitaya cladodes grown under different light conditions. **2A**, **2B**, **2C**: cross sections, abaxial face, in full sunlight; **2D**, **2E**, and **2F**: cross section, abaxial face, 80% shade. In which: ct = cuticle; e = epidermis; esm = mucilage-secreting structure; hp = hypodermis; p = parenchyma. Bars: A, B, C, D, E, F = 100 µm.

**Table 3.** Pearson's phenotypic correlation coefficients (rf) among growth characters, gas exchange, and production under conditions of full sunlight (upper diagonal) and 80% shade (lower diagonal).

| Character | *Ci* | *E* | *gs* | *A* | *A/Ci* | *A/E* | *A/gs* | SLLS | TSD | TSAT | NSLS | PROD |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Ci*** | | -0.20 | 0.52 | $0.99^{**}$ | 0.67 | 0.62 | -0.13 | 0.14 | -0.82 | -0.29 | 0.05 | 0.09 |
| ***E*** | $0.89^{*}$ | | 0.08 | -0.32 | -0.37 | $-0.89^{*}$ | -0.17 | -0.48 | 0.21 | 0.73 | 0.86 | 0.74 |
| ***gs*** | 0.15 | 0.18 | | 0.44 | 0.47 | 0.15 | $-0.91^{*}$ | 0.64 | -0.42 | -0.58 | 0.29 | -0.30 |
| ***A*** | 0.29 | 0.64 | 0.18 | | 0.69 | 0.72 | -0.03 | 0.15 | -0.82 | -0.33 | -0.07 | 0.03 |
| ***A/Ci*** | 0.15 | 0.48 | -0.25 | $0.90^{*}$ | | 0.61 | -0.16 | 0.61 | $-0.95^{*}$ | -0.54 | 0.13 | -0.38 |
| ***A/E*** | -0.72 | -0.42 | -0.02 | 0.42 | 0.51 | | 0.10 | 0.43 | -0.55 | -0.70 | -0.67 | -0.53 |
| ***A/gs*** | -0.03 | 0.10 | $-0.91^{*}$ | 0.25 | 0.62 | 0.20 | | -0.65 | 0.03 | 0.54 | -0.25 | 0.39 |
| **SCEL** | -0.61 | -0.20 | -0.15 | 0.41 | 0.46 | 0.75 | 0.32 | | -0.35 | $-0.91^{*}$ | -0.15 | $-0.89^{*}$ |
| **DET** | -0.46 | -0.52 | 0.71 | -0.20 | -0.42 | 0.36 | -0.79 | -0.05 | | 0.31 | -0.24 | 0.07 |
| **EET** | 0.50 | 0.21 | 0.21 | -0.57 | -0.73 | $-0.92^{*}$ | -0.45 | -0.61 | -0.11 | | 0.49 | $0.91^{*}$ |
| **MSPA** | -0.48 | -0.57 | 0.30 | -0.67 | -0.82 | -0.12 | -0.58 | 0.11 | 0.47 | 0.47 | -0.82 | -0.02 |
| **NEL** | 0.56 | 0.84 | 0.00 | 0.68 | 0.56 | -0.17 | 0.29 | 0.30 | -0.64 | 0.07 | | 0.53 |
| **PROD** | 0.28 | -0.12 | -0.25 | -0.44 | -0.25 | -0.50 | 0.06 | $-0.90^{*}$ | 0.00 | 0.19 | -0.56 | |

** and * significant at 1 and 5% probability by t test, respectively. The rest were not significant. Internal $CO_2$ concentration ($C_i$), stomatal conductance to water vapor (*gs*), $CO_2$ assimilation (A), transpiration (*E*), carboxylation efficiency ($A/C_i$), instantaneous efficiencies of water use (*A/E*), intrinsic (*A/gs*) efficiencies of water use, sum of the length of the cladodes (SLLS), terminal shoot diameter (TSD), terminal shoot arch thickness (TSAT), number of lateral sprouts (NLS), fruit production (PROD).

**Table 4.** Estimates of direct and indirect effects, which involve the main production variable (PROD) and the independent explanatory variables [transpiration (*E*), instant water use efficiency (*A/E*), sum of the length of lateral sprouts (SLLS), terminal shoot arch thickness (TSAT), and number of lateral sprouts (NLS)] under full sunlight and 80% shade.

| racter | Association Effects | Estimate | VIFs | | Estimate | VIFs |
|---|---|---|---|---|---|---|
| | | Full sunlight | | | 80% of shade | |
| **E** | Direct on PROD | 0.361 | 7.055 | | -0.043 | 4.841 |
| | Indirect via A/E | -0.282 | 2.620 | | 0.157 | 0.920 |
| | Indirect via SLLS | 0.273 | 1.088 | | 0.143 | 0.138 |
| | Indirect via TSAT | 0.167 | 3.295 | | -0.111 | 0.157 |
| | Indirect via NLS | 0.190 | 2.470 | | -0.261 | 3.318 |
| | Total | 0.738 | | | -0.119 | |
| **A/E** | Direct on PROD | 0.317 | 3.848 | | -0.476 | 6.315 |
| | Indirect via E | -0.322 | 4.802 | | 0.018 | 0.705 |
| | Indirect via SLLS | -0.243 | 0.867 | | -0.537 | 1.958 |
| | Indirect via TSAT | -0.161 | 3.034 | | 0.477 | 2.929 |
| | Indirect via NLS | -0.148 | 1.496 | | 0.053 | 0.136 |
| | Total | -0.532 | | | -0.501 | |
| **SLLS** | Direct on PROD | -0.564 | 5.447 | | -0.772 | 4.140 |
| | Indirect via E | -0.174 | 1.409 | | 0.009 | 0.161 |
| | Indirect via A/E | 0.137 | 0.613 | | -0.284 | 2.986 |
| | Indirect via TSAT | -0.209 | 5.149 | | 0.317 | 1.290 |
| | Indirect via NLS | -0.033 | 0.075 | | -0.093 | 0.416 |
| | Total | -0.890 | | | -0.891 | |
| **TSAT** | Direct on PROD | 0.230 | 7.253 | | -0.516 | 4.116 |
| | Indirect via E | 0.263 | 3.205 | | -0.009 | 0.185 |
| | Indirect via A/E | -0.221 | 1.610 | | 0.348 | 4.493 |
| | Indirect via SLLS | 0.514 | 3.868 | | 0.437 | 1.298 |
| | Indirect via NLS | 0.108 | 0.793 | | -0.021 | 0.021 |
| | Total | 0.912 | | | 0.189 | |
| **NLS** | Direct on PROD | 0.221 | 3.900 | | -0.310 | 5.603 |
| | Indirect via E | 0.311 | 4.469 | | -0.036 | 2.866 |
| | Indirect via A/E | -0.212 | 1.476 | | 0.064 | 0.153 |
| | Indirect via SLLS | 0.085 | 0.105 | | -0.213 | 0.308 |
| | Indirect via TSAT | 0.112 | 1.474 | | -0.035 | 0.015 |
| | Total | 0.535 | | | -0.559 | |
| **Coefficient of determination** | | 0.9282 | | | 0.8226 | |
| ***k* value used in the analysis** | | 0.0812 | | | 0.0964 | |
| **Condition number** | | 45.007 | | | 29.195 | |
| **Residual effect** | | 0.2679 | | | 0.4213 | |
| **Matrix determinant X'X** | | 0.0171 | | | 0.0368 | |

Values that inflate the variances (VIFs), transpiration (*E*), instantaneous efficiencies of water use (*A/E*), sum of the length of the cladodes (SLLS), terminal shoot arch thickness (TSAT), number of lateral sprouts (NLS), fruit production (PROD).

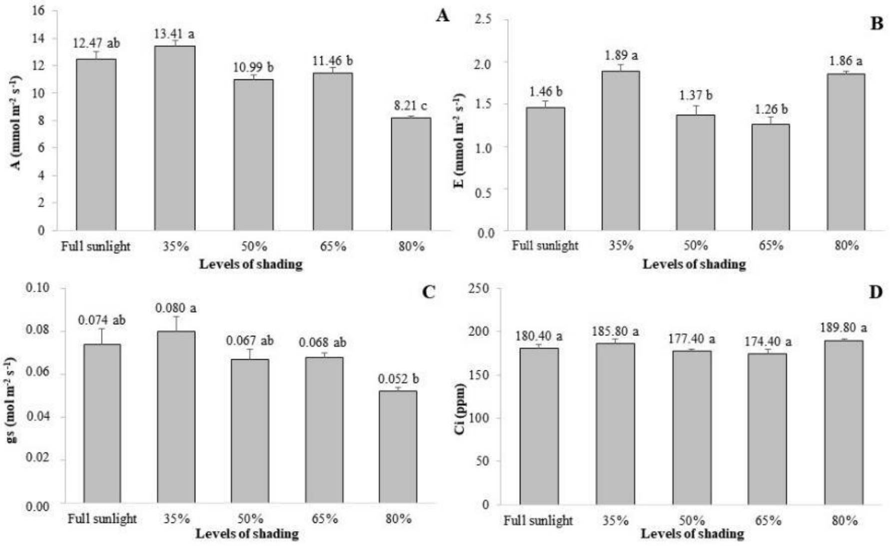


**Figure 4.** Comparison of means regarding the effect of different lighting conditions on gas exchange of red pitaya. **4A:** net carbon assimilation (*A*) (msd = 1.78); **4B**: transpiration (*E*) (msd = 0.37); **4C:** stomatal conductance to water vapor (*gs*) (msd = 0.024); **4D:** internal carbon concentration (msd = 18.18). Averages followed by the same letter do not differ by Tukey's test.

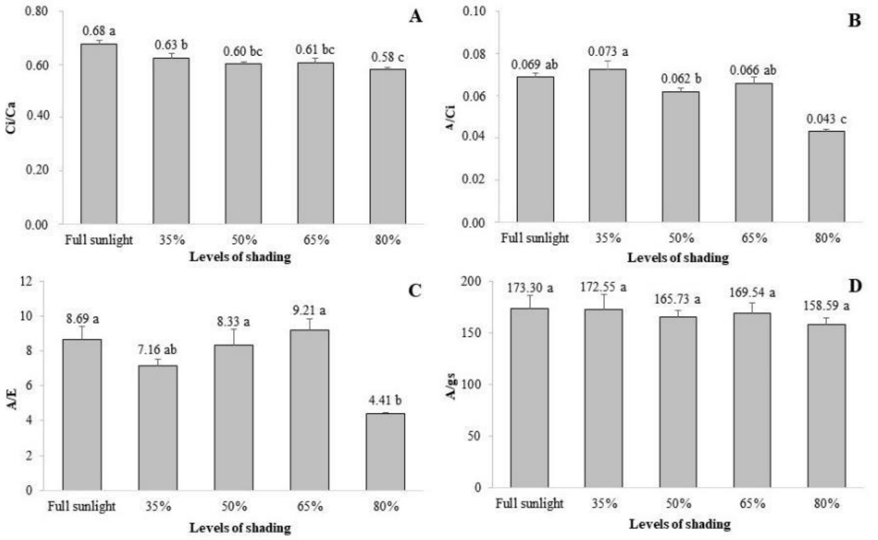


**Figure 5.** Comparison of means regarding the effect of different lighting conditions on gas exchange of red pitaya. **5A:** Ci/Ca ratio (msd = 0.035); **5B:** carboxylation efficiency (*A*/C*i*) (msd = 0.105); **5C:** instant water use efficiency (*A*/*E*) (msd = 3.00); **5D**: intrinsic water use efficiency (*A*/*gs*) (msd = 47.36). Averages followed by the same letter do not differ by Tukey's test.

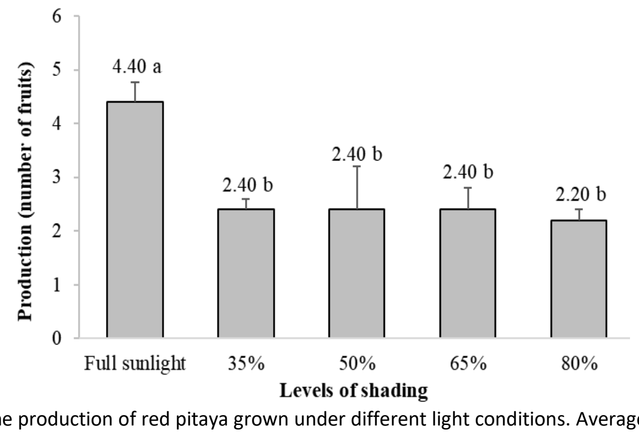


**Figure 6.** Comparison of means for the production of red pitaya grown under different light conditions. Averages followed by the same letter do not differ by Tukey's test ($p$ <0.05).

A positive association between the terminal sprout arch thickness (TSAT) and the production (PROD) was possibly due to the higher number of points for the flower's emission and, thus, of fruits. On the other hand, the negative relationship between SLLS and PROD revealed that the most productive plants were those of small size. However, under shading conditions, the vegetative growth was enhanced by the increase of photoassimilates in the expansion area for light capture, which was evidenced by the negative correlation of high magnitude between SLLS and PROD (Table 3).

Concerning correlations among vegetative characters, gas exchanges, and photosynthetic pigments, with fruit production (PROD) at 80% shading, an association of PROD with SLLS was noticed. The estimates of medium magnitude were verified between fruit production, instant water use efficiency (*A*/*E*), and the number of lateral sprouts (NLS).

It is believed that the negative correlation between A/E, SLLS, NLS, and PROD occurred due to the negative etiolation interference on production. Merten (2003), when studying cacti cultivated under different luminosity levels, mentioned this negative effect as a hypothesis for the results obtained toward growth characters.

In the path analysis, at full sunlight and 80% shading, very low values of *k* were used (Table 4). In the path analysis, at full sunlight and 80% shading, very low values of K were used (Table 4). In these two conditions, the determination coefficients varied over 80%. It indicated that a large part of the variation in fruit production was determined by the explanatory characters. In both paths analyzes, there were no values that increase the variances (VIFs) superior to 10.

According to Cruz (2013), VIFs could be used to detect the existence of multicollinearity. The occurrence of VIFs superior to ten may suggest that the regression coefficients associated with these values have estimations that are highly influenced by multicollinearity. Additionally, the condition numbers were less than 100 and indicated low collinearity. The results obtained in the present study implied that multicollinearity caused slight bias in the regression analyzes, and thus reliable estimates were obtained.

About transpiration (*E*), 0.3610 of its effect on production was positive and direct; whereas, for the number of lateral emissions, it is necessary to highlight the larger portion of indirect effects on the basic variable, mainly via perspiration (E) (Table 4). Likely, the positive effect of sweating on fruit production, in both correlations, is related to $CO_2$ absorption,

as these processes occur together with stomatal conductance. The production of photoassimilates could occur as a result of carbon fixation, which, in full sunlight, would culminate in the possibility of a greater share of carbohydrates invested in fruiting.

Regarding the unfolding of direct and indirect effects under 80% shade, it is important to highlight the negative correlation of SLLS, NLS, *E*, and *A*/*E* with PROD. Differently, cultivation in full sunlight, in which perspiration had a positive effect on the basic variable, at 80% shading, the amount of water lost by this physiological process may have been greater than the carbon uptake, which resulted in low fruiting. Additionally, under 80% shading, the increase in green mass (SLLS and NLS) may have occurred through etiolation, with drastic negative effects on fruiting. These findings are in line with the studies of Merten (2003).

## Materials and methods

### *Conduct of the study*

The experiment was carried out for a duration of 365 days, at the Horticulture Sector of the Department of Phytotechnics, of the Center of the Agricultural Sciences, belongs to the Federal University of Ceará (UFC), in Fortaleza, CE (3º43'02" S latitude and 38º32'35" WGR longitude; at altitude 19.6 m). According to the Köppen (1918) classification, the climate is Aw', rainy tropical, with an average annual temperature of 26.5 ºC.

The experimental design was in a randomized block (RDB) with five treatments (full sunlight, 35, 50, 65, and 80% shading), five replications, and two useful plants per plot. In the shading treatments, the PVC shade screens, 1.50 m wide, and dark mesh were used, placed in the extension of the cultivation line, 1.80 m from the ground, fixed in flat wire, supported with stakes and posts.

For the experiment conduction, 120-days-old red pitaya seedlings, approximately 25 cm in length, were used, as recommended by Pontes Filho et al. (2014). Propagules were collected from vigorous and healthy mother plants, two-year-old, grown in the Horticulture Sector; next, they were managed with mineral fertilizer, irrigated manually, and the crop treated for diseases, weeds, and pests.

The seedlings were transplanted "with clod" (roots surrounded by substrate) for pots of 11 $dm^3$, filled with a substrate of sand, clay, and organic matter in the proportion of 1:1:1, based on volume. The substrate presented the following initial chemical properties: O.M. – 28.86 g $kg^{-1}$; $pH_{(water)}$ – 7.0; $P_{(Mehlich\ 1)}$ – 30 mg $kg^{-1}$; $K^+$ - 1.82 $cmol_c\ dm^{-3}$; $Ca^{2+}$ - 5.8 $cmol_c\ dm^{-3}$; $Mg^{2+}$ - 2.2 $cmol_c\ dm^{-3}$; $Na^+$ - 1.72 $dm^{-3}$; $Al^{3+}$ - 0.25 $cmol_c\ dm^{-3}$; H+Al – 1.16; C/N – 10; V – 91%.

After transplanting, the pots were maintained in a greenhouse until the first sprouts emergence. Then, the plants were pruned, leaving only the most developed and best-positioned sprout. After that, the pots were transferred to field conditions. The pots were arranged at 0,70 m apart with 2.00 m between-row distance, on a base (brick) 0.10 m high. At 60 days, the plant tutoring began from sprouts, tied in 1.20 m high wooden stakes, positioned at the top of the pots.

Weed control was performed by manual weeding throughout the experimental area and also by uprooting from the pots. Irrigation was carried out in dry periods, using a localized irrigation system, applying 850 mL/day of water per pot divided into two applications of four minutes each, as recommended by Mizhari (2014) for the cultivation of *Hylocereus* in Israel.

Macro and micronutrient fertilization were held manually, solubilized in water. All doses followed the recommendations of Almeida et al. (2016b), Almeida et al. (2014), Corrêa et al. (2014) for the cultivation of *Hylocereus sp*., being used: 4.10 g $pot^{-1}$ of potassium chloride; 10.49 g triple superphosphate $vase^{-1}$; 19.67 g $vase^{-1}$ of ammonium sulfate; and 0.60 g $vase^{-1}$ of FTE BR-12. Except for the triple superphosphate and the FTE BR-12 that were applied in full amount in the transplant, the other fertilizers were divided into six equal times, applied every two months from the first month after transplanting.

***Variables analyzed***

The growth aspects studied were: terminal sprouts diameter (TSD, mm) - determined by measuring the median portion of the terminal sprouts, in the transversal direction of the cladode, with the aid of a digital caliper; terminal sprouts arch thickness (TSAT, mm) - determined by measuring the median part of the arch present in terminal cladodes, in the transversal direction of the arch, with the using a digital caliper; number of lateral sprouts (NLS, units) - determined by counting lateral cladodes; sum of the length of the cladodes - estimated by the sum of the length of the lateral sprouts (SLLS, cm), measured in the longitudinal direction of each cladode, through a measuring tape.

Gas exchanges were estimated by net $CO_2$ assimilation (A), stomatal conductance to water vapor (*gs*), transpiration (*E*), internal $CO_2$ concentration ($C_i$), ratio between internal and ambient $CO_2$ concentrations ($C_i/C_a$), in an open system and ambient $CO_2$ concentration, by a portable infrared gas analyzer (IRGA, LCi System ADC model, Bioscientific Ltd. Hoddesdon, UK).

Intrinsic (*A/gs*) and instantaneous (*A/E*) water use efficiency and the instant carboxylation efficiency ($A/C_i$) were estimated by the quotient of net carbon assimilation with stomatal conductance to water vapor, transpiration, and internal $CO_2$ concentration, respectively.

As the red pitaya is a plant with Crassulacean acid metabolism (CAM), the gas exchange evaluations were done at night, between 02:00 and 04:00 h, defined, in a previous experimental test, as the time of maximum $CO_2$ fixation, taking into consideration the conditions analyzed. The measurements were performed on mature, healthy, and vigorous cladodes. Due to their morphological characteristics, the IRGA forceps adaptation was necessary to get better analytical precision.

After gas exchange evaluations and morphological measurements, vegetative discs of 1.0 cm in diameter were collected in the central portion of mature cladodes to determine the levels of chlorophyll *a*, *b*, and total, and carotenoids, by the method described by Wellburn (1994). Furthermore, anatomical analyses were conducted in cladodes from plants grown in full sunlight and 80% shading, representing the two extremes of light. In the laboratory, transverse and longitudinal sections were made on the abaxial and adaxial faces of the cladodes.

The fruit production was estimated from the first fruiting, which occurred 186 days after the experiment installation. Whereas, the production, in units of harvested fruits, was determined by the average count of fruits harvested per plant in each plot, up to 365 days after the experiment installation.

***Statistical procedures***

The data were submitted to analysis of variance. When the null hypothesis was rejected ($p<0.05$), the means were compared using regression analysis (morphological characters) and Tukey's test (gas exchange characters, photosynthetic to anatomical pigments). The results of gas and pigment exchanges were presented in a "column" chart, composed of the means and standard errors of each treatment. These variables represent specific physiological measures.

For anatomical variables, in the sections where the measurement of the thickness of the cuticle and epidermis-hypodermis was possible, the analysis of variance was performed, just in full sunlight conditions and 80% shading (contrasting light conditions). When the null hypothesis was rejected ($p<0.05$), the means were compared using the Tukey test. In situations that it was not possible to compare the means or there was no significant statistical difference, we decided, as a form of characterization, to present the values of the means and standard error of the mean in tables.

The estimates of phenotypic correlations were obtained for the characters understood as most important in the study. Thereby, in order to unfold the correlation coefficients from medium to high magnitude, in direct and indirect effects, a single chain TRAIL analysis was performed. For the analysis, the basic variable considered was the production of fruits, and other data were admitted as explanatory variables. Thus, the correlation coefficients were unfolded under full sunlight and shading (80%) conditions.

Statistical analyzes were carried out using the statistical software Statistical Analysis System (SAS), version 9.1. The diagnoses of multicollinearity and the trail analysis were performed using a computational application of Genetics and Statistics, GENES (Cruz, 2013).

**Conclusions**

The light conditions interfere in varying degrees in the growth, anatomical structures, photosynthetic pigments, gas exchanges, production of red pitaya, and their correlations. The crop had greater phenotypic plasticity and acclimated well to full sunlight cultivation, obtaining the highest fruit production. The cultivation at 35% shading had positive effects on the net carbon assimilation and growth of red pitaya, but with production under full sunlight.

At 80% of shading, the cladodes were etiolated with antagonistic reflections on gas exchange and fruiting. Thus, it is not recommended for commercial or experimental orchards.

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