









# Photochemical activity modulated by water, nitrogen, and phosphorus status in cactus pear

Marcos Neves Lopes<sup>1\*</sup> , Gil Mario Ferreira Gomes<sup>2</sup> , Theyson Duarte Maranhão<sup>3</sup> , Walisson Marques Silveira<sup>4</sup> , Roberto Cláudio Fernandes Franco Pompeu<sup>5</sup> , Rodrigo Gregório da Silva<sup>6</sup> , Marlos Alves Bezerra<sup>7</sup> , Magno José Duarte Cândido<sup>8</sup> 

- <sup>1</sup> Instituto Federal de Educação, Ciência e Tecnologia do Piauí, Campus Valença do Piauí, Valença do Piauí, PI, Brasil.
- <sup>2</sup> Instituto Federal de Educação, Ciência e Tecnologia do Piauí, Campus Paulistana, Paulistana, PI, Brasil.
- <sup>3</sup> Universidade de São Paulo, Escola Superior de Agricultura “Luiz de Queiroz”, Piracicaba, SP, Brasil.
- <sup>4</sup> Universidade Federal do Ceará, Departamento de Engenharia Agrícola, Fortaleza, CE, Brasil.
- <sup>5</sup> Empresa Brasileira de Pesquisa Agropecuária - Embrapa Caprinos e Ovinos, Sobral, CE, Brasil.
- <sup>6</sup> Instituto Federal de Educação, Ciência e Tecnologia do Ceará, Campus Limoeiro do Norte, Limoeiro do Norte, CE, Brasil.
- <sup>7</sup> Empresa Brasileira de Pesquisa Agropecuária - Embrapa Agroindústria Tropical, Fortaleza, CE, Brasil.
- <sup>8</sup> Universidade Federal do Ceará, Departamento de Zootecnia, Fortaleza, CE, Brasil.

\*Corresponding author:  
marcos.neves@ifpi.edu.br

Received: January 26, 2021

Accepted: April 27, 2021

**How to cite:** Lopes, M. N.; Gomes, G. M. F.; Maranhão, T. D.; Silveira, W. M.; Pompeu, R. C. F. F.; Silva, R. G.; Bezerra, M. A. and Cândido, M. J. D. 2021. Photochemical activity modulated by water, nitrogen, and phosphorus status in cactus pear. *Revista Brasileira de Zootecnia* 50:e20210012.  
<https://doi.org/10.37496/rbz5020210012>

**Copyright:** This is an open access article distributed under the terms of the Creative Commons Attribution License (<http://creativecommons.org/licenses/by/4.0/>), which permits unrestricted use, distribution, and reproduction in any medium, provided the original work is properly cited.



**ABSTRACT** - This study aimed to evaluate the effects of nitrogen (N) and phosphorus (P) associated with dry and rainy seasons on the photochemical activity of *Opuntia ficus-indica* (L.) Mill. cv. Gigante. Combinations of N (10.0, 70.0, 100.0, 130.0, and 190.0 kg ha<sup>-1</sup> yr<sup>-1</sup>) and P<sub>2</sub>O<sub>5</sub> (10.0, 70.0, 100.0, 130.0, and 190.0 kg ha<sup>-1</sup> yr<sup>-1</sup>) were evaluated in the dry and rainy seasons in semi-arid regions. A completely randomized block design with split-plot arrangement was adopted with four replications. In Quixadá, the maximum potential quantum efficiency of photosystem II (Fv/Fm) was 0.82, observed in third-order cladodes (rainy season and N/P 75.6/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup>), while in Tejuçuoca, the maximum Fv/Fm was 0.81, found in 2nd/3rd order cladodes (rainy season and N/P 10.0/190.0 kg ha<sup>-1</sup> yr<sup>-1</sup>). In Quixadá, the maximum electron transport rate (ETR) was 31.6 μmol m<sup>-2</sup> s<sup>-1</sup> in 2nd/3rd order cladodes (rainy season and N/P 10.0/190.0 kg ha<sup>-1</sup> yr<sup>-1</sup>), and in Tejuçuoca, the maximum ETR was 24.1 μmol m<sup>-2</sup> s<sup>-1</sup>, in second-order cladodes (rainy season and N/P 110.1/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup>). In Quixadá and Tejuçuoca, higher values of Fv/Fm and ETR were observed in the rainy season. In Quixadá, the maximum fluorescence decrease ratio (FDR) was 4.04 in third-order cladodes (rainy season and N/P 10.0/114.8 kg ha<sup>-1</sup> yr<sup>-1</sup>), while in Tejuçuoca, the maximum FDR was 6.93, found in 2nd/3rd order cladodes (rainy season and N/P 190.0/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup>). In Quixadá and Tejuçuoca, there was predominance of higher FDR values in the rainy season. Nitrogen, phosphorus, and water status modulate the photochemical efficiency of cladodes of cactus pear cv. Gigante in semi-arid regions.

**Keywords:** effective quantum efficiency of PSII, electron transport rate, fertilization, water stress

## 1. Introduction

Cactus pear belongs to the group of crassulacean acid metabolism (CAM) plants (Ranson and Thomas, 1960). This is an important mechanism for the adaptation of these plants to arid and semi-arid regions,

associated with the features of stomatal diurnal closure and nocturnal opening, which minimizes water losses (Nobel, 2002) and confers high efficiency in the use of water (Silva et al., 2014; Lopes et al., 2018a; Souza et al., 2019).

Fertilization with nitrogen and phosphorus has shown effects on biomass flow and accumulation, water use efficiency (Lopes et al., 2018a), and productivity of cactus pear (Dubeux Jr. et al., 2006), as well as the proven influence on the accumulation and export of nutrients in forage biomass (Lopes et al., 2018b). Moreover, the positive effect of nitrogen is highlighted on gas exchanges, with increments in the photosynthetic rate (Pompeu et al., 2010; Lopes et al., 2011a; Silva et al., 2016) and elevation of growth rates, biomass flow, and productivity of different forage plants (Lopes et al., 2011b,c; Lopes et al., 2013), besides the positive relationship of N with the assimilation of CO<sub>2</sub> in hemiepiphytic cactus (Nobel and De la Barrera, 2002). Thus, the combined effects of N and P on the morphophysiological characteristics of cactus pear may be the influence of nutrients in some stage of the photosynthetic process, influencing the photosynthetic efficiency of the forage crop in the soil and climatic conditions of cultivation.

The analysis of photochemical activity has been proposed in the study of physiological responses of plants because it is a non-destructive method, which allows the quantitative evaluation of absorption and use of the light energy through photosystem II (PSII) and the possible relationships with the photosynthetic capacity of the plant (Ferraz et al., 2014). Studies on physiology of forage plants are important to leverage scientific and technological development in the field of plant production, as they allow the identification of environmental and management conditions that increase the photochemical efficiency of plants.

Thus, this study was carried out to evaluate the effect of combined levels of N and P, associated with the effect of dry and rainy seasons, on the photochemical activity of different types of cladodes of the cactus pear (*Opuntia ficus-indica* (L.) Mill.) cv. Gigante, in semi-arid regions.

## 2. Material and Methods

### 2.1. Experimental sites

The experiment was carried out during 2013 and 2014 in the municipalities of Quixadá [(4°59' S, 39°01' W, 190 m a.s.l., BSw'h' climate, hot semi-arid (Koppen, 1948)] and Tejuçuoca [(3°59' S, 39°34' W, 140 m a.s.l., Aw climate, tropical with dry season (Koppen, 1948)], located in the semi-arid region of the state of Ceará, Brazil.

In both regions, data on average temperature (T) and air relative humidity (RH) of the experimental period and soil moisture ( $\theta$ ) were recorded in the dry and rainy seasons. In Quixadá, 27.0 °C and 58.8% were observed for T and RH, respectively. In Tejuçuoca, the values were 26.4 °C and 65.5% for T and RH, respectively. Data were obtained at the Agro-climatological Station. In Quixadá,  $\theta$  of 0.0038 and 0.081 cm<sup>3</sup> cm<sup>-3</sup> was recorded in the dry and rainy seasons, respectively. In Tejuçuoca, the values of  $\theta$  recorded in the dry and rainy seasons were 0.0113 and 0.192 cm<sup>3</sup> cm<sup>-3</sup>, respectively.

Soil analysis presented the following results for Quixadá and Tejuçuoca, respectively (layer 0.0-20.0 cm): 6.1 and 6.2 soil pH (in water), 5.0 and 6.0 mg kg<sup>-1</sup> P (extraction with Mehlich-1), 260.0 and 243.0 mg kg<sup>-1</sup> K (extraction with Mehlich-1), 20.0 and 7.0 mg kg<sup>-1</sup> Na, 34.0 and 40.0 mmol<sub>c</sub> kg<sup>-1</sup> Ca (extraction with KCl 1 mol L<sup>-1</sup>), 34.0 and 32.0 mmol<sub>c</sub> kg<sup>-1</sup> Mg (extraction with KCl 1 mol L<sup>-1</sup>), 0.0 and 0.0 mmol<sub>c</sub> kg<sup>-1</sup> Al (extraction with KCl 1 mol L<sup>-1</sup>), 5.3 and 8.2 g kg<sup>-1</sup> organic matter (colorimetric method), 75.5 and 78.5 mmol<sub>c</sub> kg<sup>-1</sup> sum of bases, and 75.5 and 78.5 mmol<sub>c</sub> kg<sup>-1</sup> effective cation exchange capacity. The soil texture analysis presented 513 and 164 g kg<sup>-1</sup> coarse sand, 363 and 590 g kg<sup>-1</sup> fine sand, 89 and 153 g kg<sup>-1</sup> silt, and 35 and 93 g kg<sup>-1</sup> clay in Quixadá and Tejuçuoca, respectively. Analyses were performed following the Embrapa's (Brazilian Agricultural Research Corporation) method of soil analysis.

## 2.2. Orchard establishment and plant material

Soil preparation for planting cactus pear cv. Gigante in the agricultural year of 2011 included the following steps: removal of stumps (whenever necessary), removal of vegetation from the area, and harrowing. Then, plots were marked for delimitation of the area. Each plot was 24.0 m<sup>2</sup> in area (4.0 × 6.0 m), consisting of 120 plants, distributed in three 4.0-m-long rows, using the central row for measurements and the side rows as borders. After harvesting, cladodes were allowed to rest in a shaded area for fifteen days to heal damages caused during harvest and transportation.

Furrows were made by hand using cutter mattock, narrow hoe, and hoe, at an average depth of 30 cm and spacing of 2.0 m. Cladodes were placed at a depth that provided their coverage in 2/3, with spacing of 2.0 × 0.10 m, which is the recommendation to reach a density of 50,000 plants ha<sup>-1</sup>.

## 2.3. Mineral fertilization matrix and experimental design

Nine combinations of N and P levels were studied, which consisted of five levels of N (10.0, 70.0, 100.0, 130.0, and 190.0 kg ha<sup>-1</sup> yr<sup>-1</sup>) as urea and five levels of P<sub>2</sub>O<sub>5</sub> (10.0, 70.0, 100.0, 130.0, and 190.0 kg ha<sup>-1</sup> year<sup>-1</sup>) as single superphosphate, according to the matrix Plan Puebla II, for two factors (2<sup>k</sup> + 2k + 1) (Turrent Fernández and Laird, 1975). The adopted standard combinations (central point) were N (100 kg ha<sup>-1</sup> yr<sup>-1</sup>) and P<sub>2</sub>O<sub>5</sub> (100.0 kg ha<sup>-1</sup> yr<sup>-1</sup>), and from that, the other combinations were defined according to fixed levels of ±0.3 (30%) and ±0.9 (90%).

The nine N and P<sub>2</sub>O<sub>5</sub> combinations evaluated were: N10.0P<sub>2</sub>O<sub>5</sub>70.0 (10.0 kg N and 70.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N70.0P<sub>2</sub>O<sub>5</sub>10.0 (70.0 kg N and 10.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N70.0P<sub>2</sub>O<sub>5</sub>70.0 (70.0 kg N and 70.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N70.0P<sub>2</sub>O<sub>5</sub>130.0 (70.0 kg N and 130.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N100.0P<sub>2</sub>O<sub>5</sub>100.0 (100.0 kg N and 100.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N130.0P<sub>2</sub>O<sub>5</sub>70.0 (130.0 kg N and 70.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N130.0P<sub>2</sub>O<sub>5</sub>130.0 (130.0 kg N and 130.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), N130.0P<sub>2</sub>O<sub>5</sub>190.0 (130.0 kg N and 190.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>), and N190.0P<sub>2</sub>O<sub>5</sub>130.0 (190.0 kg N and 130.0 kg P<sub>2</sub>O<sub>5</sub> ha<sup>-1</sup> yr<sup>-1</sup>). These N and P combinations were studied in two seasons (dry and rainy) and three types of cladodes, with four replications, distributed in a completely randomized block design with split-plot arrangement, in which the combinations of N and P levels were assigned to plots, types of cladodes to subplots, and seasons (dry and rainy) to sub-subplots.

The statistical model used in the experiment was the following (1):

$$Y_{ijkl} = \mu + B_k + D_i + \alpha_{(i)k} + C_j + DC_{ij} + e_{(ij)} + P_1 + DP_{ij} + CP_{il} + DCP_{ijl} + \varepsilon_{ijkl} \quad (1)$$

in which  $\mu$  = overall mean,  $B_k$  = effect of block,  $D_i$  = effect of fertilization,  $\alpha_{(i)k}$  = error of plot (error A),  $C_j$  = effect of cladode,  $DC_{ij}$  = effect of fertilization × cladode interaction,  $e_{(ij)}$  = error of subplot (error B),  $P_1$  = effect of season,  $DP_{ij}$  = effect of fertilization × season interaction,  $CP_{il}$  = effect of the cladode × season interaction,  $DCP_{ijl}$  = effect of the fertilization × cladode × season interaction, and  $\varepsilon_{ijkl}$  = residual error.

## 2.4. Mineral fertilization program

Fertilization was carried out during the rainy season. The annual level of P, as single superphosphate, was provided at once, upon planting in the first year (fertilizer applied in the planting furrow) and when the rainy season began in the other years (fertilizer applied in the crop planting row, with 20 cm spacing from the basal cladodes). At this time, micronutrients were applied at a level of 50 kg ha<sup>-1</sup> FTE BR-12. The balancing of calcium and sulfur was done for all treatments, using agricultural gypsum and calcitic limestone, based on the highest level of single superphosphate.

The annual N level, as urea, was provided in three applications, with a 20-day interval. In all applications, urea was diluted in water, applying 1.0 L of the solution to every 4-m row, totalizing the volume of 3.0 L per plot. Dilution was made to better standardize the application, due to the small amount of fertilizer per plot in some levels, making it difficult to apply in the solid form. Weed control was manually performed with herbicide (non-selective herbicide, with post-emergence systemic action of the chemical group – substituted glycine, with soluble concentrate formulation type) in directed jet. The control of cochineal (*Diaspis echinocacti*) was carried out using mineral oil.

## 2.5. Response variables

From the N and P combinations described above, responses of the photochemical activity of cactus pear were evaluated in the dry (210 days after cutting) and rainy (350 days after cutting) seasons, in different types of cladodes (second-order cladodes without the presence of third-order cladodes, second-order cladodes with the presence of third-order cladodes, and third-order cladodes). Readings were carried out using a portable fluorometer (Multi-Mode Chlorophyll Fluorometer) OS5p model (Opti-Sciences, USA), in the morning, starting at 9.00 h. The instrument was calibrated (according to the procedures recommended by the manufacturer's guide) in a pre-trial for the cactus pear crop under the same conditions that the readings were taken. Evaluations were performed in cladodes previously adapted to the dark (using leaf clips for 30 min) (Lin et al., 2003). The following variables were analyzed: potential (Fv/Fm) and effective ( $\Phi_{\text{PSII}}$ ) quantum efficiencies of PSII, electron transport rate (ETR,  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ), and fluorescence decrease ratio (FDR = [Fm - Ft]/Ft).

## 2.6. Data analysis

Data were analyzed according to the responses pattern. Qualitative factors (types of cladodes and seasons of the year) were compared in a descriptive way, from the graphical analysis and observation of the mean and standard error. Quantitative factors (N and P levels) were analyzed using multiple regression models. Selection of models was based on the significance of parameters ( $P < 0.001$ ,  $P < 0.01$ ,  $P < 0.05$ , and  $P < 0.10$ , corresponding to the symbols \*\*\*, \*\*, \*, and  $\Delta$ , respectively) and on the coefficient of determination. The computer software SAEG 9.1 (2007) was used for data analysis.

## 3. Results

### 3.1. Potential (Fv/Fm) and effective ( $\Phi_{\text{PSII}}$ ) quantum efficiency of PSII

When evaluating Fv/Fm and  $\Phi_{\text{PSII}}$  in the dry and rainy seasons, in the different types of cactus pear cladodes in Quixadá and Tejuçuoca, a significant effect of the combined fertilizations with N and P was found, fitting a multiple regression model ( $P < 0.001$ ,  $P < 0.01$ ,  $P < 0.05$ , and  $P < 0.10$ ; Table 1).

In Quixadá, the estimations showed values of Fv/Fm from 0.50 in 2nd/3rd order cladodes (dry season,  $P < 0.001$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 10.0/190.0 kg ha<sup>-1</sup> yr<sup>-1</sup> to 0.82 in third-order cladodes (rainy season,  $P < 0.01$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 75.6/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup>. For the combined fertilization of 114.6 and 136.8 kg ha<sup>-1</sup> yr<sup>-1</sup> N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production), Fv/Fm was estimated at 0.61 for 2nd/3rd order cladodes in the dry season, and 0.71 and 0.81 for third-order cladodes in the dry and rainy seasons, respectively. In Tejuçuoca, the estimates showed Fv/Fm values varying from 0.48 in 2nd/3rd order cladodes (dry season,  $P < 0.01$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 190.0/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup> to 0.81 in 2nd/3rd order cladodes (rainy season,  $P < 0.05$ ) and N/P combination of 10.0/190.0 kg ha<sup>-1</sup> yr<sup>-1</sup>. For the combined levels of 190.0 and 56.8 kg ha<sup>-1</sup> yr<sup>-1</sup> of N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production), Fv/Fm was estimated at 1.0 for second-order cladodes in the dry season; 0.55 and 0.77 for 2nd/3rd order cladodes in the dry and rainy seasons, respectively; and 0.78 for third-order cladodes in the rainy season.

Higher Fv/Fm values were observed in the rainy season for the different types of cactus pear cladodes, in Quixadá (Figure 1A) and Tejuçuoca (Figure 1B), and the different N and P combinations. In Quixadá and Tejuçuoca, the positive effect of greater soil moisture in the rainy season on Fv/Fm can also be seen in the averages of N and P combinations. In Quixadá, Fv/Fm values were 0.65 (dry season) and 0.81 (rainy season), 0.63 (dry season) and 0.78 (rainy season), and 0.70 (dry season) and 0.81 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively. In Tejuçuoca, Fv/Fm values were 0.66 (dry season) and 0.80 (rainy season), 0.64 (dry season) and 0.79 (rainy season), and 0.69 (dry season) and 0.79 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively.

In general, when analyzing the Fv/Fm ratio in cactus pear cladodes subjected to water deficit (dry season), in Quixadá (Figure 1A) and Tejuçuoca (Figure 1B), there was a superiority in Fv/Fm values in third-order cladodes.

In Quixadá, the estimated  $\Phi_{PSII}$  ranged from 0.0 in second-order cladodes (dry season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 165.3/37.8 kg ha<sup>-1</sup> yr<sup>-1</sup> to 0.62 in 2nd/3rd order cladodes (rainy season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 190.0/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup>. For the combined fertilization of 114.6 and 136.8 kg ha<sup>-1</sup> yr<sup>-1</sup> of N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production), the estimated values of  $\Phi_{PSII}$  for second-order cladodes were 0.18 and 0.53 in the dry and rainy seasons, respectively; 0.14 and 0.43 for 2nd/3rd order cladodes in the dry and rainy seasons, respectively; and 0.23 for third-order cladodes in the dry season. In Tejuçuoca,  $\Phi_{PSII}$  estimates varied from 0.04 in second-order cladodes (dry season,  $P < 0.001$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 10.0/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup> to 0.48 in second-order cladodes (rainy season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 110.0/10.0 kg ha<sup>-1</sup> yr<sup>-1</sup>. For the combined levels of 190.0 and 56.8 kg ha<sup>-1</sup> yr<sup>-1</sup> of N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production),  $\Phi_{PSII}$  estimates for second-order cladodes were 0.42 and 0.42 in the dry and rainy seasons, respectively; 0.17 for 2nd/3rd order cladodes in the dry season; and 0.18 and 0.35 for third-order cladodes in the dry and rainy seasons, respectively.

**Table 1** - Potential (Fv/Fm) and effective ( $\Phi_{PSII}$ ) quantum efficiencies of PSII in the dry and rainy seasons of different cactus pear cladodes according to N and P fertilization, in Quixadá and Tejuçuoca

Region <sup>1</sup>	Season <sup>2</sup>	Cladode <sup>3</sup>	Model <sup>4</sup>
QUIX	Dry	2nd	Fv/Fm = 0.648
		2nd/3rd	Fv/Fm = 0.674255 + 0.000552096N - 0.000951608P; R <sup>2</sup> = 0.72***
		3rd	Fv/Fm = 0.59503 + 0.00044198N + 0.0017732P - 0.000009607P <sup>2</sup> ; R <sup>2</sup> = 0.55**
	Rainy	2nd	Fv/Fm = 0.80
		2nd/3rd	Fv/Fm = 0.78
		3rd	Fv/Fm = 0.822 + 0.000104N - 0.000000686N <sup>2</sup> - 0.000293P + 0.00000135P <sup>2</sup> ; R <sup>2</sup> = 0.72**
TEJ	Dry	2nd	Fv/Fm = 0.66
		2nd/3rd	Fv/Fm = 0.80718 - 0.0018019N - 0.00171887P + 0.000016609NP; R <sup>2</sup> = 0.76**
		3rd	Fv/Fm = 0.69
	Rainy	2nd	Fv/Fm = 0.80
		2nd/3rd	Fv/Fm = 0.788169 - 0.000136523N + 0.000140021P; R <sup>2</sup> = 0.50*
		3rd	Fv/Fm = 0.76416 + 0.0002303N - 0.00000106204N <sup>2</sup> + 0.0001062P; R <sup>2</sup> = 0.49 <sup>4</sup>
QUIX	Dry	2nd	$\Phi_{PSII} = 0.201 - 0.00077N - 0.0000069N^2 + 0.00026P - 0.0000091P^2 + 0.000019NP$ ; R <sup>2</sup> = 0.58*
		2nd/3rd	$\Phi_{PSII} = 0.18236 + 0.000644N - 0.000002398N^2 - 0.00138P + 0.00000547P^2$ ; R <sup>2</sup> = 0.84***
		3rd	$\Phi_{PSII} = 0.097584 + 0.00052078N + 0.0016853P - 0.00000827P^2$ ; R <sup>2</sup> = 0.75***
	Rainy	2nd	$\Phi_{PSII} = 0.2054 + 0.00172N - 0.00000971N^2 + 0.004128P - 0.0000165P^2$ ; R <sup>2</sup> = 0.89***
		2nd/3rd	$\Phi_{PSII} = 0.361868 + 0.00143045N + 0.00101543P - 0.000014846NP$ ; R <sup>2</sup> = 0.32*
		3rd	$\Phi_{PSII} = 0.47$
TEJ	Dry	2nd	$\Phi_{PSII} = 0.0196 + 0.0014N + 0.000013N^2 + 0.00096P + 0.0000165P^2 - 0.000043NP$ ; R <sup>2</sup> = 0.69***
		2nd/3rd	$\Phi_{PSII} = 0.212 - 0.000535N + 0.00000273N^2 - 0.000837P + 0.00000349776P^2$ ; R <sup>2</sup> = 0.71**
		3rd	$\Phi_{PSII} = 0.285884 - 0.0016675N + 0.0000053367N^2 + 0.00031282P$ ; R <sup>2</sup> = 0.43**
	Rainy	2nd	$\Phi_{PSII} = 0.40406 + 0.0014509N - 0.00000659663N^2 - 0.000459774P$ ; R <sup>2</sup> = 0.63*
		2nd/3rd	$\Phi_{PSII} = 0.38$
		3rd	$\Phi_{PSII} = 0.4616 - 0.0012288N + 0.00000395N^2 - 0.000564P + 0.00000374P^2$ ; R <sup>2</sup> = 0.44 <sup>4</sup>

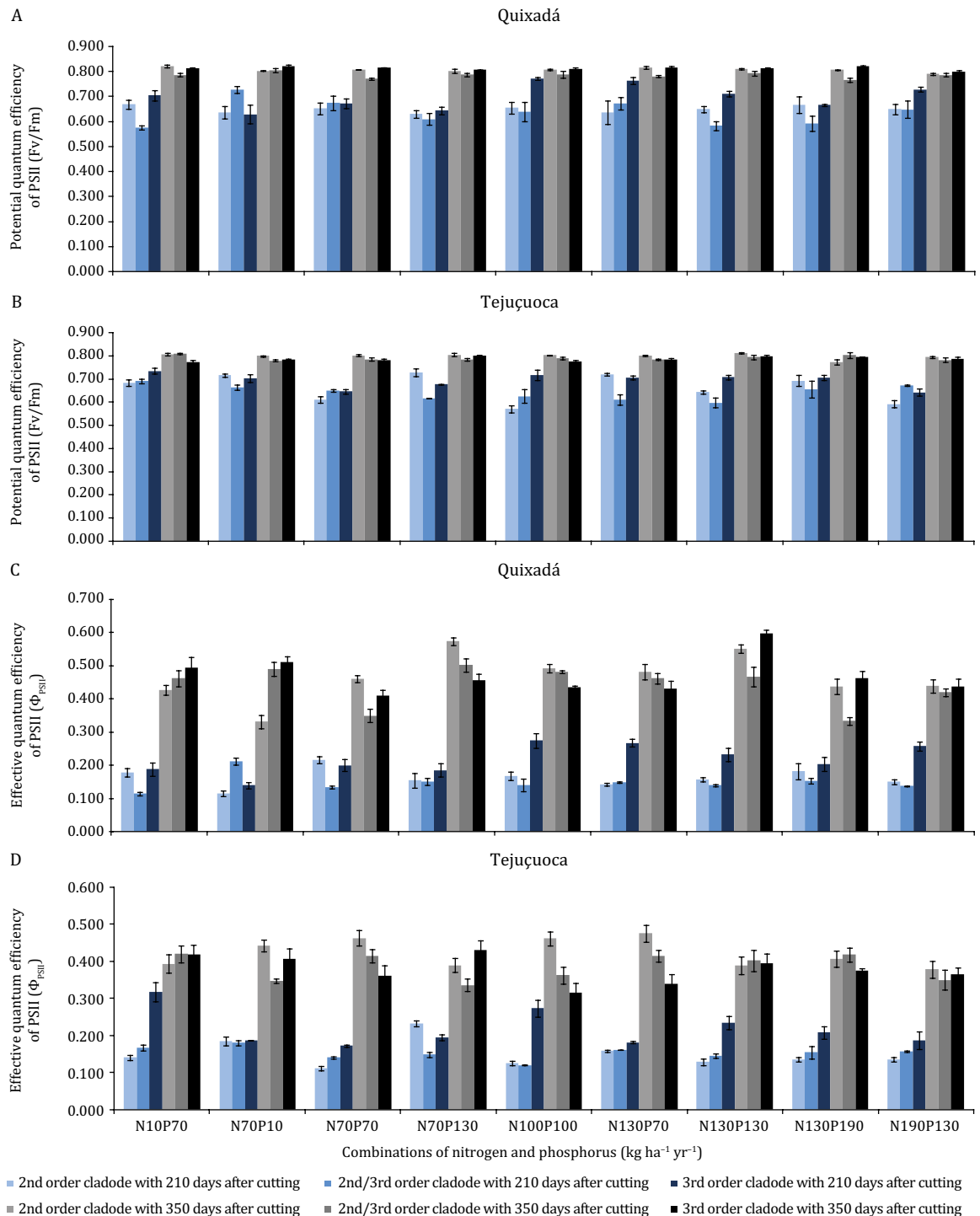
<sup>1</sup> Quixadá (QUIX) and Tejuçuoca (TEJ); N = kg ha<sup>-1</sup> yr<sup>-1</sup> N and P = kg ha<sup>-1</sup> yr<sup>-1</sup> P<sub>2</sub>O<sub>5</sub>.

<sup>2</sup> Dry season (210 days after cutting) and rainy season (350 days after cutting).

<sup>3</sup> Second-order (2nd) cladodes, second-order cladodes with the presence of third-order cladodes (2nd/3rd), and third-order (3rd) cladodes.

<sup>4</sup> Significant at  $P < 0.001$  (\*\*\*),  $P < 0.01$  (\*\*),  $P < 0.05$  (\*), and  $P < 0.10$  (<sup>4</sup>).

In the evaluation of  $\Phi_{\text{PSII}}$  between the different orders of cactus pear cladodes, in the soil and climatic conditions of Quixadá (Figure 1C) and Tejuçuoca (Figure 1D), and in the different N and P combinations, higher  $\Phi_{\text{PSII}}$  values for the three types of cladodes were observed in the rainy season. The effect of seasons in Quixadá and Tejuçuoca can be seen in the averages of N and P combinations. In Quixadá,



Evaluations carried out in October 2013 (dry season, 210 days after cutting) and March 2014 (rainy season, 350 days after cutting) in the regions of Quixadá and Tejuçuoca; N =  $\text{kg ha}^{-1} \text{ yr}^{-1}$  N and P =  $\text{kg ha}^{-1} \text{ yr}^{-1} \text{ P}_2\text{O}_5$ . Each column represents the treatment mean ( $n = 4$ ) and bars represent the standard error of the mean.

**Figure 1** - Potential and effective quantum efficiencies of PSII in cladodes of cactus pear cv. Gigante fertilized with N and P in the dry and rainy seasons in Quixadá (A and C) and Tejuçuoca (B and D).

$\Phi_{PSII}$  values were 0.16 (dry season) and 0.47 (rainy season), 0.15 (dry season) and 0.44 (rainy season), and 0.22 (dry season) and 0.47 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively. In Tejuçuoca,  $\Phi_{PSII}$  values were 0.15 (dry season) and 0.42 (rainy season), 0.15 (dry season) and 0.38 (rainy season), and 0.22 (dry season) and 0.39 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively.

Differences in  $\Phi_{PSII}$  values between the types of cactus pear cladodes were observed in Quixadá and in Tejuçuoca, in the different N and P combinations during dry and rainy seasons. For most N and P combinations, when  $\Phi_{PSII}$  was evaluated in cactus pear cladodes under conditions of water deficit (dry season) in the two regions (Figures 1C and D), a superiority was found in third-order cladodes. In the rainy season, a fluctuation was observed regarding the superiority of  $\Phi_{PSII}$  values between the different types of cladodes, which depended on the region (Figures 1C and D) and fertilization management.

### 3.2. Electron transport rate (ETR) and fluorescence decrease ratio (FDR)

In the analyses of ETR and FDR in the dry and rainy seasons and in the different types of cactus pear cladodes in Quixadá and Tejuçuoca, a significant effect of the combined N and P levels was detected, fitting a multiple regression model ( $P < 0.001$ ,  $P < 0.01$ ,  $P < 0.05$ , and  $P < 0.10$ ; Table 2).

**Table 2** - Electron transport rate (ETR) and fluorescence decrease ratio (FDR) of different cladodes of cactus pear according to combined N and P fertilization in the dry and rainy seasons in Quixadá and Tejuçuoca

Region <sup>1</sup>	Season <sup>2</sup>	Cladode <sup>3</sup>	Model <sup>4</sup>
QUIX	Dry	2nd	ETR = 10.04 - 0.038N - 0.00035N <sup>2</sup> + 0.014P - 0.00045P <sup>2</sup> + 0.000928NP; R <sup>2</sup> = 0.57*
		2nd/3rd	ETR = 10.24 + 0.00856224N - 0.0746528P + 0.000301569P <sup>2</sup> ; R <sup>2</sup> = 0.76***
		3rd	ETR = 4.89 + 0.0261728N + 0.0846565P - 0.000415875P <sup>2</sup> ; R <sup>2</sup> = 0.75***
	Rainy	2nd	ETR = 10.30 + 0.0867N - 0.0004879N <sup>2</sup> + 0.2079P - 0.0008331P <sup>2</sup> ; R <sup>2</sup> = 0.89***
		2nd/3rd	ETR = 17.53 + 0.04951N + 0.000265N <sup>2</sup> + 0.08169P - 0.00105445NP; R <sup>2</sup> = 0.38*
		3rd	ETR = 23.6
TEJ	Dry	2nd	ETR = 7.5
		2nd/3rd	ETR = 10.62 - 0.027057N + 0.00013786N <sup>2</sup> - 0.041311P + 0.0001722P <sup>2</sup> ; R <sup>2</sup> = 0.70**
		3rd	ETR = 14.39 - 0.0843521N + 0.00027218N <sup>2</sup> + 0.0154138P; R <sup>2</sup> = 0.43**
	Rainy	2nd	ETR = 20.34 + 0.0725578N - 0.000329456N <sup>2</sup> - 0.0232716P; R <sup>2</sup> = 0.63*
		2nd/3rd	ETR = 19.3
		3rd	ETR = 23.25 - 0.062248N + 0.00020219N <sup>2</sup> - 0.028637P + 0.00018753P <sup>2</sup> ; R <sup>2</sup> = 0.44 <sup>Δ</sup>
QUIX	Dry	2nd	FDR = 2.16 - 0.0061847N + 0.000024152N <sup>2</sup> + 0.00492422P; R <sup>2</sup> = 0.74***
		2nd/3rd	FDR = 2.25
		3rd	FDR = 2.18
	Rainy	2nd	FDR = 3.43
		2nd/3rd	FDR = 3.22
		3rd	FDR = 3.147 - 0.0058144N + 0.0145455P - 0.0000556198P <sup>2</sup> ; R <sup>2</sup> = 0.77***
TEJ	Dry	2nd	FDR = 2.68
		2nd/3rd	FDR = 3.27 - 0.00945708N - 0.0114139P + 0.000104425NP; R <sup>2</sup> = 0.64*
		3rd	FDR = 2.25 + 0.01287N - 0.00005161N <sup>2</sup> - 0.01155P + 0.0000493P <sup>2</sup> ; R <sup>2</sup> = 0.61***
	Rainy	2nd	FDR = 3.38 - 0.00243293N - 0.00154442P; R <sup>2</sup> = 0.43**
		2nd/3rd	FDR = 1.94 + 0.018N + 0.000056N <sup>2</sup> + 0.0027P + 0.00012P <sup>2</sup> - 0.00027NP; R <sup>2</sup> = 0.83***
		3rd	FDR = 3.13 + 0.00228054N - 0.00392794P; R <sup>2</sup> = 0.26 <sup>Δ</sup>

<sup>1</sup> Quixadá (QUIX) and Tejuçuoca (TEJ); N = kg ha<sup>-1</sup> yr<sup>-1</sup> N and P = kg ha<sup>-1</sup> yr<sup>-1</sup> P<sub>2</sub>O<sub>5</sub>.

<sup>2</sup> Dry season (210 days after cutting) and rainy season (350 days after cutting).

<sup>3</sup> Second-order (2nd) cladodes, second-order cladodes with the presence of third-order cladodes (2nd/3rd), and third-order (3rd) cladodes.

<sup>4</sup> Significant at P < 0.001 (\*\*\*), P < 0.01 (\*\*), P < 0.05 (\*), and P < 0.10 (<sup>Δ</sup>).

In Quixadá, estimated ETR values ranged from 0.0  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in second-order cladodes (dry season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 165.4/37.8  $\text{kg ha}^{-1} \text{yr}^{-1}$  to 31.6  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 2nd/3rd order cladodes (rainy season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 10.0/190.0  $\text{kg ha}^{-1} \text{yr}^{-1}$ . For the combined fertilization of 114.6 and 136.8  $\text{kg ha}^{-1} \text{yr}^{-1}$  of N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production), ETR was estimated at 9.1 and 26.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for second-order cladodes in the dry and rainy seasons, respectively; 6.7 and 21.3  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for 2nd/3rd order cladodes in the dry and rainy seasons, respectively; and 11.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for third-order cladodes in the dry season. In Tejuçuoca, estimated ETR values ranged from 6.8  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in 2nd/3rd order cladodes (dry season,  $P < 0.01$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 98.1/120.1  $\text{kg ha}^{-1} \text{yr}^{-1}$  to 24.1  $\mu\text{mol m}^{-2} \text{s}^{-1}$  in second-order cladodes (rainy season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 110.1/10.0  $\text{kg ha}^{-1} \text{yr}^{-1}$ . For the N and P<sub>2</sub>O<sub>5</sub> combination of 190.0 and 56.8  $\text{kg ha}^{-1} \text{yr}^{-1}$ , respectively (levels for maximum biomass production), ETR estimates were 21.2 and 20.9  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for second-order cladodes in the dry and rainy seasons, respectively; 8.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for 2nd/3rd order cladodes in the dry season; and 9.1 and 17.7  $\mu\text{mol m}^{-2} \text{s}^{-1}$  for third-order cladodes in the dry and rainy seasons, respectively.

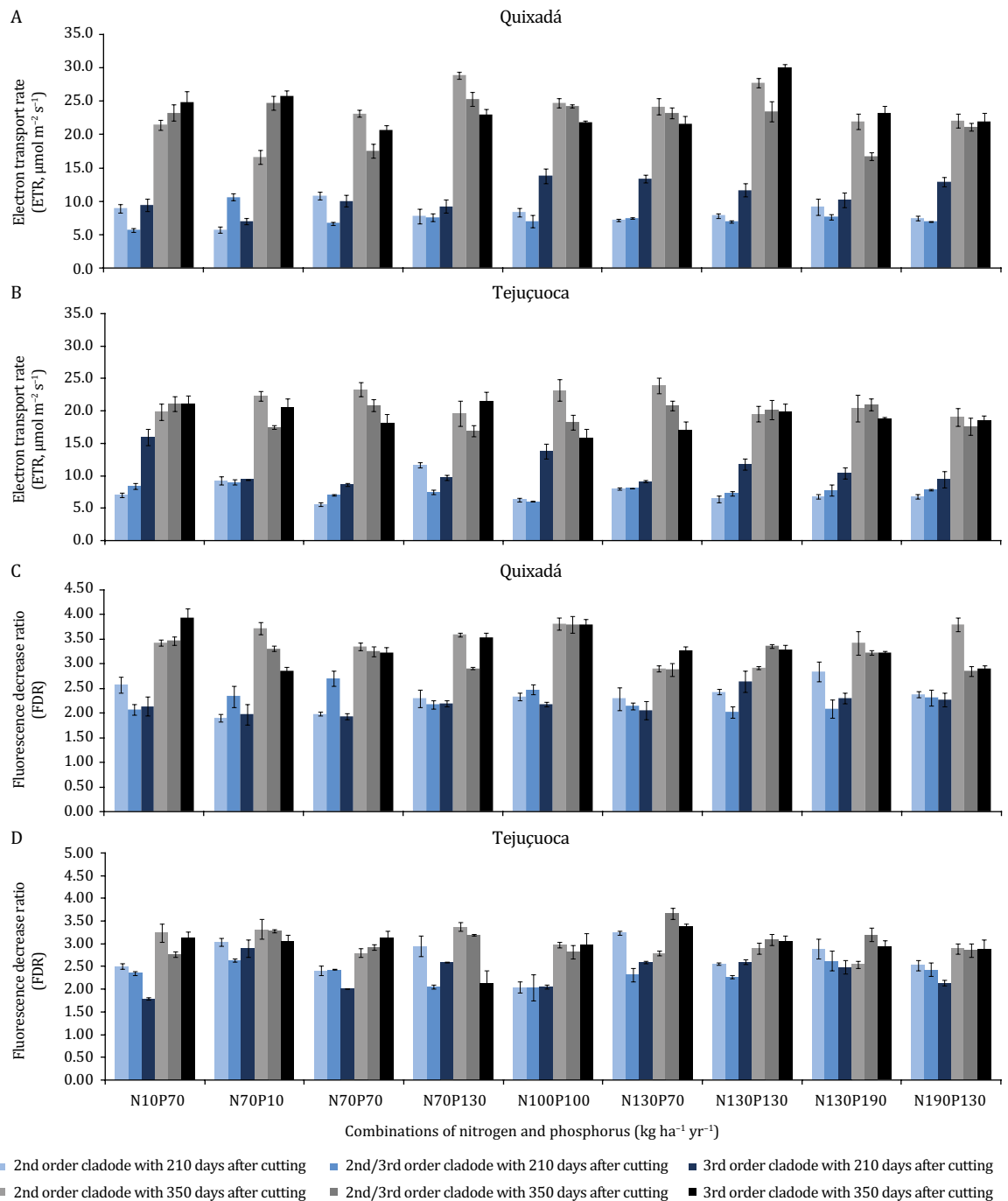
In Quixadá (Figure 2A) and Tejuçuoca (Figure 2B), in the nine N and P combinations, higher values of ETR were observed in the three types of cladodes in the rainy season. In Quixadá, in the average of N and P combinations, ETR values were 8.1 (dry season) and 23.4 (rainy season), 7.4 (dry season) and 22.1 (rainy season), and 10.8 (dry season) and 23.6 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively. In Tejuçuoca, in the average of N and P combinations, ETR values were 7.5 (dry season) and 21.2 (rainy season), 7.6 (dry season) and 19.3 (rainy season), and 10.9 (dry season) and 19.0 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively.

In the assessment of ETR in cactus pear cladodes under water deficit conditions (dry season), in most N and P combinations, in both Quixadá (Figure 2A) and Tejuçuoca (Figure 2B), there was a superiority of ETR in third-order cladodes. In the rainy season, there was a shift in the order of superiority of ETR values between the types of cladodes, depending on soil and climatic conditions and fertilization management.

In Quixadá, FDR estimates ranged from 1.81 in second-order cladodes (dry season,  $P < 0.001$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 128.0/10.0  $\text{kg ha}^{-1} \text{yr}^{-1}$  to 4.04 in third-order cladodes (rainy season,  $P < 0.001$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 10.0/114.8  $\text{kg ha}^{-1} \text{yr}^{-1}$ . For the combined fertilization of 114.6 and 136.8  $\text{kg ha}^{-1} \text{yr}^{-1}$  of N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production), FDR was estimated at 2.44 for second-order cladodes in the dry season, 3.38 for 2nd/3rd order cladodes in the rainy season, and 3.43 for third-order cladodes in the rainy season. In Tejuçuoca, the estimated FDR values ranged from 1.20 in 2nd/3rd order cladodes (dry season,  $P < 0.05$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 10.0/190.0  $\text{kg ha}^{-1} \text{yr}^{-1}$  to 6.93 in 2nd/3rd order cladodes (rainy season,  $P < 0.001$ ) and N/P<sub>2</sub>O<sub>5</sub> combination of 190.0/10.0  $\text{kg ha}^{-1} \text{yr}^{-1}$ . For the combination of 190.0 and 56.8  $\text{kg ha}^{-1} \text{yr}^{-1}$  of N and P<sub>2</sub>O<sub>5</sub>, respectively (levels for maximum biomass production), FDR estimates were 5.59 and 2.83 for second-order cladodes in the dry and rainy seasons, respectively; 1.95 and 4.98 for 2nd/3rd order cladodes in the dry and rainy seasons, respectively; and 2.33 and 3.34 for third-order cladodes in the dry and rainy seasons, respectively.

In Quixadá (Figure 2C), in the different cladode types and in all N and P combinations, FDR values showed superiority in the rainy season. In the average of N and P combinations, FDR values were 2.33 (dry season) and 3.43 (rainy season), 2.25 (dry season) and 3.22 (rainy season), and 2.18 (dry season) and 3.33 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively. In Tejuçuoca (Figure 2D), there was also predominance of higher FDR values in the rainy season. In the average of N and P combinations, FDR values were estimated at 2.68 (dry season) and 2.98 (rainy season), 2.35 (dry season) and 3.09 (rainy season), and 2.35 (dry season) and 2.96 (rainy season) for second-order, 2nd/3rd order, and third-order cladodes, respectively. In both Quixadá and Tejuçuoca, in the different combinations of fertilization and in the two evaluated seasons, there were variations in FDR values between the different types of cladodes (Figures 2C and D).





Evaluations carried out in October 2013 (dry season, 210 days after cutting) and March 2014 (rainy season, 350 days after cutting) in the regions of Quixadá and Tejuçuoca; N =  $\text{kg ha}^{-1} \text{yr}^{-1}$  N and P =  $\text{kg ha}^{-1} \text{yr}^{-1}$  P<sub>2</sub>O<sub>5</sub>. Each column represents the treatment mean (n = 4) and bars represent the standard error of the mean.

**Figure 2** - Electron transport rate and fluorescence decrease ratio in cladodes of cactus pear cv. Gigante fertilized with N and P in Quixadá (A and C) and Tejuçuoca (B and D).

## 4. Discussion

### 4.1. Potential ( $F_v/F_m$ ) and effective ( $\Phi_{\text{PSII}}$ ) quantum efficiency of PSII

The quantification of the effect of N and P on  $F_v/F_m$  and  $\Phi_{\text{PSII}}$  of the cactus pear photosystem II allows the identification of the status of these nutrients, which increases the photochemical efficiency of PSII when all of its reaction centers are open, under different environmental and management conditions.

Studying the quantum yield of cactus pear genotypes of the genera *Opuntia* spp. and *Nopalea* spp., Souza et al. (2019) reported values of Fv/Fm ranging from 0.77 to 0.82, allowing the authors to identify the genotype F16 (Fv/Fm = 0.77) as the least efficient in the capture of the excitation energy by the reaction centers of PSII. In general, according to Reis and Campostrini (2011), Fv/Fm values between 0.75 and 0.85 indicate plants with the photosynthetic apparatus intact, while Fv/Fm values lower than 0.75 indicate a reduction in plant photosynthetic potential. Thus, it can be inferred from the estimated Fv/Fm results of cactus pear in Quixadá and Tejuçuoca that the balanced N and P combinations, especially in that soil moisture conditions (rainy season), provided adequate responses of the quantum yield of the evaluated crop.

The variation in the Fv/Fm ratio in the different types of cladodes in the two evaluated seasons (dry and rainy) as a response to N and P<sub>2</sub>O<sub>5</sub> fertilization is supported by changes in initial fluorescence (F<sub>0</sub>) and maximum fluorescence (Fm) of cactus pear fertilized with combined levels of N and P. The responses in favor of Fv/Fm of cactus pear under different conditions of cultivation and combined N and P levels suggest that the fertilization had a positive effect on the use of the absorbed energy and on dissipation efficiency, also acting in a beneficial way on the photochemical machinery of cladode tissues of the cactus pear. In addition, it is worth mentioning that fertilization with P promotes an increase in nutrient content in the cladode, which may positively reflect on Fv/Fm and  $\Phi_{\text{PSII}}$ , once according to Singh and Reddy (2014), the increase in P content in the plant tissue affects different photochemical characteristics (Fv/Fm,  $\Phi_{\text{PSII}}$ , ETR etc.) and the photosynthetic rate of the crop.

The  $\Phi_{\text{PSII}}$  represents an estimation of light use efficiency by the plant for the transport of electrons in PSII (Singh et al., 2013). In the different treatments for the different types of cactus pear cladodes under combined N and P levels,  $\Phi_{\text{PSII}}$  followed the dynamics of Fv/Fm and Fv/F<sub>0</sub> responses in plants subjected to N and P<sub>2</sub>O<sub>5</sub> fertilization, demonstrating more detectable changes in the electron transport efficiency, which was confirmed by the behavior of ETR values in the different cladodes and management conditions of the crop.

The reduction observed in the Fv/Fm ratio in the dry season (Figures 1A and B) and in the different types of cladodes in Quixadá and Tejuçuoca in cactus pear plants fertilized with different N and P combinations confirms the negative influence of water deficit on the Fv/Fm ratio, as documented by Masrahi et al. (2012), who studied *Caralluma* (Apocynaceae) species in arid conditions and by Mattos et al. (1999), who evaluated the CAM plant *Clusia minor* under conditions of prolonged water deficit. Low Fv/Fm values in plants under water deficit indicate a reduction in the efficiency of the PSII antenna complex and the effective quantum yield of PSII (Sayed, 2003). Moreover, the reduction in PSII activity under water shortage, which characterizes a strong stress, can be attributed to the excess of energization of PSII during phase III in CAM plants, which occurs under closed stomata conditions and in the presence of high irradiance and high temperature (Niewiadomska and Borland, 2008).

In the different types of cladodes, under the nine N and P combinations, the lower  $\Phi_{\text{PSII}}$  values observed in the dry season characterized the negative effect of water deficit on this variable, as observations showed the decrease of electron transport efficiency (Lin et al., 2003). Reductions observed in the Fv/Fm ratio as well as  $\Phi_{\text{PSII}}$  in plants under water deficit (dry season) cause decreases in the PSII antenna system efficiency and PSII quantum yield (Sayed, 2003). In this context, a reduction of PSII activity, represented by the decrease in Fv/Fm and  $\Phi_{\text{PSII}}$  values, was also observed by Mattos et al. (1999), but for the CAM plant *Clusia minor* under conditions of prolonged water stress.

The superiority of Fv/Fm values in third-order cladodes may be an indication that these cladodes under water deficit conditions can present efficient non-photochemical energy dissipation, probably influenced by the presence of zeaxanthin, which exerts photoprotective action on the light harvesting complexes of PSII (Horton et al., 1996).

#### 4.2. Electron transport rate (ETR) and fluorescence decrease ratio (FDR)

The observed variations in the ETR in different cactus pear cladodes in the dry and rainy seasons, under the different environmental conditions and combined N and P levels might be a result of alterations

in thylakoids of chloroplasts as well as modifications related to photosystems I and II. The action of nutrients on ETR may reflect on the photosynthetic activity of the forage plant (Konrad et al., 2005), and it can be confirmed by the dynamics of the ETR curve under photosynthetic photon flux (PPF), which presents the same response pattern of CO<sub>2</sub> assimilation as a function of the PPF (Bilger et al., 1995), allowing the conclusion that a suitable combination of N and P under conditions of good water availability in the soil may increase the ETR for CO<sub>2</sub> assimilation by the forage crop. Importantly, the increase in N and P contents in plant tissues may alter the ETR due to the positive relationship between P content and ETR (Singh and Reddy, 2014), and it is also worth mentioning the correlation between the contents of chlorophyll and N in the tissues of hemi-epiphytic cactus with the net capacity of CO<sub>2</sub> assimilation (Nobel and De la Barrera, 2002).

The estimations indicated that the balanced fertilization of N and P resulted in values of FDR higher than 2.5, allowing to infer that the balanced management of nutrient availability favored the good functioning of the photosynthetic process. The improvement observed in FDR might favor growth through gains in biomass flow (Lopes et al., 2018a), reflecting positively on cactus pear productivity (Dubeux Jr. et al., 2006), responding through the beneficial action of N on assimilation in CAM plants (Nobel and De la Barrera, 2002). As N and P combinations favored vitality indices (FDR) in the cactus pear crop, depending on the environmental conditions, the evaluated seasons (dry and rainy) and the parts of the plant under analysis, it can be inferred that the conversion of radiant energy into chemical energy and its use in the biochemical phase of the photosynthesis were more efficient, which will positively influence the photosynthetic process, with an increase in the net photosynthesis rate of the crop.

Regarding the ETR responses in plants under stress, it is worth highlighting situations that promote reductions in electron transport, such as inhibition of water photolysis, reduction of energy capture efficiency by the PSII reaction centers, changes in electron flux after quinone A (leaf temperature, LT > 42 °C), and PSI damage (LT > 45 °C; Havaux, 1993), which greatly affect the photosynthetic process in plants. With respect to water deficit conditions in CAM plants, it should be mentioned that changes in Fm and Fv values of *Opuntia ficus-indica* cladode tissues under water deficit resulted in changes in the activity of the electron photosynthetic transport. In addition, certain stress factors, such as high temperatures (Schreiber and Berry, 1977) or severe water deficit (Becerril and Valdivia, 2006), may influence the activity of enzymes involved in the carbon reduction process, also affecting the electron photosynthetic transport. Becerril and Valdivia (2006) reported that under severe water deficit, the PEPcase activity was reduced by 20 and 60% in chlorenchyma and parenchyma tissues, respectively, in comparison with the management without water limitation in the soil.

In this context, physiological changes related to enzymatic activities in CAM plants, such as energy flow and use, water flow, and gas exchange, are related to the degree of stress caused by water deficit (von Willert et al., 1992). Under severe water limitation, mature *Opuntia ficus-indica* cladodes close the stomata, which may cause changes in PEPcase activity (Acevedo et al., 1983). In addition, these physiological modifications may also be related to changes in protein synthesis that are induced by water deficit.

Variation in ETR between the types of cactus pear cladodes under the environmental conditions of Quixadá and Tejuçuoca can be related to the partition between the chlorenchyma and parenchyma and, consequently, the photochemical activity of each tissue, depending on the fertilization management and evaluated seasons (dry and rainy). According to Becerril and Valdivia (2006), the electron photosynthetic transport in the chlorenchyma of cladodes of plants under good soil moisture conditions was eleven times more active than in the parenchyma. Under severe water deficit, the photochemical activity (ETR) in chlorenchyma was reduced by 29% and the ETR in the parenchyma more than doubled when compared with the treatment without water restriction in the soil. Thus, the higher activity of electron photosynthetic transport in chlorenchyma of cladodes of plants without water limitation confirms that this photochemical activity occurs mainly in chlorenchyma chloroplasts (Becerril and Valdivia, 2006). It is also worth mentioning that the decrease in the photosynthetic electron transport activity in the chlorenchyma of cladodes of plants under severe water deficit can also result from the effect of other

alterations, such as a more prolonged stomatal closure (Acevedo et al., 1983), which probably will alter photosynthetic activities, especially the biochemical reduction of CO<sub>2</sub> (Peña-Valdivia, 1994).

In all types of cladodes, higher FDR values in the rainy season point to the relevance of adequate water supply for better photochemical efficiency of cactus pear, which results in good photosynthetic activity of the crop, without compromising CO<sub>2</sub> assimilation. The observed variations in FDR values between the three types of cladodes, in the different fertilization managements, in dry and rainy seasons, in Quixadá and Tejuçuoca, followed by changes in the other chlorophyll fluorescence variables, allow the conclusion that the crop photochemical activity presented a magnitude of different responses according to the part of the plant analyzed, a fact that indicates photosynthetic changes in the different types of cladodes.

## 5. Conclusions

This research produced relevant knowledge about the joint effects of multiple factors, such as fertilization, water availability, and soil and climatic conditions on the photochemical activity of different cactus pear cladodes of the cv. Gigante cultivated in semi-arid regions of Brazil.

The fertilization management with combined levels of nitrogen and phosphorus modifies the photochemical activity in different types of cactus pear cladodes of the cv. Gigante, in both dry and rainy seasons of the growth cycle, in semi-arid regions of Brazil.

The water stress experienced by the cactus pear cv. Gigante during the dry season in the two regions studied changed the photochemical responses, with noticeable effects on the potential and effective quantum efficiencies of PSII and electron transport rate. Cactus pear cv. Gigante fertilized with nitrogen and phosphorus and cultivated in dry and rainy seasons, under the soil and climatic conditions of the Brazilian semi-arid region, presents variations in the photochemical activity between the different orders of cladodes.

## Conflict of Interest

The authors declare no conflict of interest.

## Author Contributions

Conceptualization: M.N. Lopes, R.G. Silva and M.J.D. Cândido. Formal analysis: M.N. Lopes and M.J.D. Cândido. Funding acquisition: M.J.D. Cândido. Investigation: M.N. Lopes, G.M.F. Gomes, T.D. Maranhão, W.M. Silveira, R.C.F.F. Pompeu, R.G. Silva, M.A. Bezerra and M.J.D. Cândido. Methodology: M.N. Lopes, G.M.F. Gomes, T.D. Maranhão, W.M. Silveira, R.C.F.F. Pompeu, R.G. Silva, M.A. Bezerra and M.J.D. Cândido. Project administration: M.N. Lopes and M.J.D. Cândido. Supervision: R.C.F.F. Pompeu and M.J.D. Cândido. Visualization: M.N. Lopes, G.M.F. Gomes, T.D. Maranhão, R.C.F.F. Pompeu, R.G. Silva and M.J.D. Cândido. Writing-original draft: M.N. Lopes and M.J.D. Cândido. Writing-review & editing: M.N. Lopes and M.J.D. Cândido.

## References

- Acevedo, E.; Badilla, I. and Nobel, P. S. 1983. Water relations, diurnal acidity changes, and productivity of a cultivated cactus, *Opuntia ficus-indica*. *Plant Physiology* 72:775-780. <https://doi.org/10.1104/pp.72.3.775>
- Becerril, G. A. and Valdivia, C. B. P. 2006. Physiological alterations induced by drought stress on prickly pear (*Opuntia ficus-indica*). *Revista Fitotecnia Mexicana* 29:231-237.
- Bilger, W.; Schreiber, U. and Bock, M. 1995. Determination of the quantum efficiency of photosystem II and non-photochemical quenching of chlorophyll fluorescence in the field. *Oecologia* 102:425-432. <https://doi.org/10.1007/BF00341354>
- Dubeux Jr, J. C. B.; Santos, M. V. F.; Lira, M. A.; Santos, D. C.; Farias, I.; Lima, L. E. and Ferreira, R. L. C. 2006. Productivity of *Opuntia ficus-indica* (L.) Miller under different N and P fertilization and plant population in north-east Brazil. *Journal of Arid Environments* 67:357-372. <https://doi.org/10.1016/j.jaridenv.2006.02.015>

- Ferraz, R. L. S.; Beltrão, N. E. M.; Melo, A. S.; Magalhães, I. D.; Fernandes, P. D. and Rocha, M. S. 2014. Trocas gasosas e eficiência fotoquímica de cultivares de algodoeiro herbáceo sob aplicação de silício foliar. *Semina: Ciências Agrárias* 35:735-748. <https://doi.org/10.5433/1679-0359.2014v35n2p735>
- Havaux, M. 1993. Rapid photosynthetic adaptation to heat stress triggered in potato leaves by moderately elevated temperatures. *Plant, Cell & Environment* 16:461-467. <https://doi.org/10.1111/j.1365-3040.1993.tb00893.x>
- Horton, P.; Ruban, A. V. and Walters, R. G. 1996. Regulation of light harvesting in green plants. *Annual Review of Plant Physiology and Plant Molecular Biology* 47:655-684. <https://doi.org/10.1146/annurev.arplant.47.1.655>
- Konrad, M. L. F.; Silva, J. A. B.; Furlani, P. R. and Machado, E. C. 2005. Trocas gasosas e fluorescência da clorofila em seis cultivares de cafeeiro sob estresse de alumínio. *Bragantia* 64:339-347. <https://doi.org/10.1590/S0006-87052005000300004>
- Koppen, W. 1948. *Climatologia: con un estudio de los climas de la tierra*. Fondo de Cultura Económica, Mexico. 478p.
- Lin, Z. F.; Peng, C. L. and Lin, G. Z. 2003. Photooxidation in leaves of facultative CAM plant *Sedum spectabile* at C<sub>3</sub> and CAM mode. *Acta Botanica Sinica* 45:301-306.
- Lopes, M. N.; Lacerda, C. F.; Cândido, M. J. D.; Pompeu, R. C. F. F.; Silva, R. G.; Lopes, J. W. B.; Fernandes, F. R. B. and Bezerra, F. M. L. 2011a. Gas exchange in massai grass under five nitrogen fertilization levels during establishment and regrowth. *Revista Brasileira de Zootecnia* 40:1862-1869. <https://doi.org/10.1590/S1516-35982011000900004>
- Lopes, M. N.; Pompeu, R. C. F. F.; Cândido, M. J. D.; Lacerda, C. F.; Silva, R. G. and Fernandes, F. R. B. 2011b. Growth index in massai grass under different levels of nitrogen fertilization. *Revista Brasileira de Zootecnia* 40:2666-2672. <https://doi.org/10.1590/S1516-35982011001200008>
- Lopes, M. N.; Cândido, M. J. D.; Pompeu, R. C. F. F.; Silva, R. G.; Lopes, J. W. B. and Bezerra, F. M. L. 2011c. Biomass components in Massai grass during establishment and regrowth under five nitrogen fertilization levels. *Revista Brasileira de Zootecnia* 40:1629-1637. <https://doi.org/10.1590/S1516-35982011000800002>
- Lopes, M. N.; Cândido, M. J. D.; Pompeu, R. C. F. F.; Silva, R. G.; Carvalho, T. C. F.; Sombra, W. A.; Moraes Neto, L. B. and Peixoto, M. J. A. 2013. Biomass flow in massai grass fertilized with nitrogen under intermittent stocking grazing with sheep. *Revista Brasileira de Zootecnia* 42:13-21. <https://doi.org/10.1590/S1516-35982013000100003>
- Lopes, M. N.; Cândido, M. J. D.; Gomes, E. C.; Pompeu, R. C. F. F. and Silva, R. G. 2018a. Biomass flow and water efficiency of cactus pear under different managements in the Brazilian Semiarid. *Revista Ciência Agronômica* 49:324-333.
- Lopes, M. N.; Cândido, M. J. D.; Silveira, W. M.; Maranhão, T. D.; Soares, I.; Pompeu, R. C. F. F.; Silva, R. G. and Carneiro, M. S. S. 2018b. Accumulation and export of nutrients in cactus pear cladodes (*Opuntia ficus-indica*) under different managements in the Brazilian Semiarid. *Revista Brasileira de Zootecnia* 47:e20170077. <https://doi.org/10.1590/rbz4720170077>
- Masrahi, Y. S.; Al-Turki, T. A. and Sayed, O. H. 2012. Crassulacean acid metabolism permutation and survival of *Caralluma* species (Apocynaceae) in arid habitats. *Ecologia Balkanica* 4:63-71.
- Mattos, E. A.; Herzog, B. and Lüttge, U. 1999. Chlorophyll fluorescence during CAM-phases in *Clusia minor* L. under drought stress. *Journal of Experimental Botany* 50:253-261.
- Niewiadomska, E. and Borland, A. M. 2008. Crassulacean acid metabolism: a cause or consequence of oxidative stress in planta? p.247-266. In: *Progress in botany*. vol. 69. Lüttge, U.; Beyschlag, W. and Murata, J., eds. Springer, Berlin. [https://doi.org/10.1007/978-3-540-72954-9\\_10](https://doi.org/10.1007/978-3-540-72954-9_10)
- Nobel, P. S. 2002. *Cacti: biology and uses*. University of California Press, Berkeley.
- Nobel, P. S. and De la Barrera, E. 2002. Nitrogen relations for net CO<sub>2</sub> uptake by the cultivated hemiepiphytic cactus, *Hylocereus undatus*. *Scientia Horticulturae* 96:281-292. [https://doi.org/10.1016/S0304-4238\(02\)00060-2](https://doi.org/10.1016/S0304-4238(02)00060-2)
- Peña-Valdivia, C. B. 1994. Functional effects of mild water stress on young *Phaseolus vulgaris* L. plant. *Plant Physiology* 13:125-134.
- Pompeu, R. C. F. F.; Cândido, M. J. D.; Lopes, M. N.; Gomes, F. H. T.; Lacerda, C. F.; Aquino, B. F. and Magalhães, J. A. 2010. Características morfofisiológicas do capim-aruana sob diferentes doses de nitrogênio. *Revista Brasileira de Saúde e Produção Animal* 11:1187-1210.
- Ranson, S. L. and Thomas, M. 1960. Crassulacean acid metabolism. *Annual Review of Plant Physiology* 11:81-110. <https://doi.org/10.1146/annurev.pp.11.060160.000501>
- Reis, F. O. and Campostrini, E. 2011. Microaspersão de água sobre a copa: um estudo relacionado às trocas gasosas e à eficiência fotoquímica em plantas de mamoeiro. *Revista Brasileira de Agrociência* 17:66-77.
- Sayed, O. H. 2003. Chlorophyll fluorescence as a tool in cereal crop research. *Photosynthetica* 41:321-330. <https://doi.org/10.1023/B:PHOT.0000015454.36367.e2>
- Schreiber, U. and Berry, J. A. 1977. Heat-induced changes of chlorophyll fluorescence in intact leaves correlated with damage of the photosynthetic apparatus. *Planta* 136:233-238. <https://doi.org/10.1007/BF00385990>

- Silva, L. M.; Fagundes, J. L.; Viegas, P. A. A.; Muniz, E. N.; Rangel, J. H. A.; Moreira, A. L. and Backes, A. A. 2014. Produtividade da palma forrageira cultivada em diferentes densidades de plantio. *Ciência Rural* 44:2064-2071. <https://doi.org/10.1590/0103-8478cr20131305>
- Silva, V. J.; Pedreira, C. G. S.; Sollenberger, L. E.; Silva, L. S.; Yasuoka, J. I. and Almeida, I. C. L. 2016. Carbon assimilation, herbage plant-part accumulation, and organic reserves of grazed 'Mulato II' *Brachiariagrass* pastures. *Crop Science* 56:2853-2860. <https://doi.org/10.2135/cropsci2016.03.0148>
- Singh, S. K.; Badgujar, G.; Reddy, V. R.; Fleisher, D. H. and Bunce, J. A. 2013. Carbon dioxide diffusion across stomata and mesophyll and photo-biochemical processes as affected by growth CO<sub>2</sub> and phosphorus nutrition in cotton. *Journal of Plant Physiology* 170:801-813. <https://doi.org/10.1016/j.jplph.2013.01.001>
- Singh, S. K. and Reddy, V. R. 2014. Combined effects of phosphorus nutrition and elevated carbon dioxide concentration on chlorophyll fluorescence, photosynthesis, and nutrient efficiency of cotton. *Journal of Plant Nutrition and Soil Science* 177:892-902. <https://doi.org/10.1002/jpln.201400117>
- Souza, J. T. A.; Ribeiro, J. E. S.; Ramos, J. P. F.; Sousa, W. H.; Araújo, J. S.; Lima, G. F. C. and Dias, J. A. 2019. Rendimento quântico e eficiência de uso da água de genótipos de palma forrageira no Semiárido brasileiro. *Archivos de Zootecnia* 68:268-273. <https://doi.org/10.21071/az.v68i262.4146>
- Turrent Fernández, A. and Laird, R. J. 1975. La matriz experimental Plan Puebla, para ensayos sobre prácticas de producción de cultivos. *Agrociencia* 19:117-143.
- von Willert, D. J.; Eller, B. M.; Werger, M. J. A.; Brinckmann, E. and Ihlenfeldt, H. D. 1992. Life strategies of succulents in deserts: with special reference to the Namib desert. Cambridge University Press, Cambridge. p.155-275.