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Gas exchange, photosynthetic pigments, and photochemical efficiency of sesame under salt stress and phosphate fertilization

Trocas gasosas, pigmentos fotossintéticos e eficiência fotoquímica do gergelim sob estresse salino e adubação fosfatada

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Highlights

Sesame cv. BRS Seda is sensitive to salt stress.
Water salinity above 0.3 dS m^{-1} reduces the growth of sesame plants.
The water salinity of 3.5 dS m^{-1} does not change intercellular CO_2 concentration.

Abstract

Salt stress is a threat to irrigated agriculture, especially in semi-arid regions, as it can cause irreversible damage to the photosynthetic apparatus at any stage of plant development, reducing chlorophyll biosynthesis, which compromises the photochemical efficiency and the photosynthetic process of plants. In this respect, phosphorus fertilization stands out as an alternative to mitigate the effects of salt stress on plants. Therefore, the present study investigated the growth, gas exchange, photosynthetic pigments, and photochemical efficiency of sesame cv. BRS Seda irrigated with saline water and fertilized with phosphorus. The experiment was carried out in pots adapted as lysimeters in a greenhouse in Pombal - PB, Brazil. Treatments were distributed in randomized blocks and analyzed in a 5 × 4 factorial arrangement with five levels of electrical conductivity of water (ECw: 0.3, 1.1, 1.9, 2.7, and 3.5 dS m^{-1}) and four phosphorus rates (40, 70, 100, and 130% of the recommended dose for pot trials), in three replicates. The 100%

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recommendation consisted of applying 300 mg P_2O_5 kg^{-1} of soil. Sesame growth, chloroplast pigments, and gas exchange decreased with water salinity above 0.3 dS m^{-1}. The application of 100 and 130% of the recommended phosphorus rate minimized the effects of salt stress on CO_2 assimilation rate and photosynthetic pigment synthesis. The increase from 40 to 130% of the recommended phosphorus rate did not change the photochemical efficiency of sesame cv. BRS Seda at 60 days after sowing.

Key words: Chlorophyll content. Phosphorus rates. Photosynthesis. Saline waters.

Resumo

O estresse salino constitui ameaça à agricultura irrigada, sobretudo em regiões semiáridas, pois pode causar danos irreversíveis ao aparato fotossintético em qualquer estágio de desenvolvimento da planta, com redução na biossíntese de clorofila, o que compromete a eficiência fotoquímica e o processo fotossintético das plantas. Como alternativa para mitigar os efeitos do estresse salino nas plantas destaca-se a adubação com fósforo. Assim, objetivou-se avaliar o crescimento, as trocas gasosas, os pigmentos fotossintéticos e a eficiência fotoquímica do gergelim cv. BRS Seda irrigado com águas salinas e adubação fosfatada. O experimento foi conduzido em vasos adaptados como lisímetros em casa de vegetação em Pombal-PB. Os tratamentos foram distribuídos em blocos ao acaso e analisados em esquema fatorial 5 × 4, sendo cinco níveis de condutividade elétrica da água - CEa (0,3; 1,1; 1,9; 2,7 e 3,5 dS m^{-1}) e quatro doses de fósforo (40, 70, 100 e 130% da recomendação para ensaios em vasos) com três repetições. A recomendação de 100% consistiu em aplicação de 300 mg de P_2O_5 kg^{-1} de solo. O crescimento, os pigmentos cloroplastídicos e as trocas gasosas do gergelim foram reduzidos com a salinidade da água acima de 0,3 dS m^{-1}. Os efeitos do estresse salino sobre a taxa de assimilação de CO_2 e a síntese de pigmentos fotossintéticos foram minimizados com a aplicação de 100 e 130% da recomendação de fósforo. O aumento de 40 para 130% da recomendação de fósforo não alterou a eficiência fotoquímica do gergelim cv. BRS Seda aos 60 dias após a semeadura.

Palavras-chave: Doses de fósforo. Águas salinas. Fotossíntese. Teor de clorofila.

Introduction

Sesame (*Sesamum indicum* L.), a member of the family Pedaliaceae, originated in the African continent. This species plays a social role in the rural environment, as it is grown mainly by small- and medium-sized farmers, in addition to being an option for regions prone to water scarcity thanks to its resistance to drought (Araújo, Borges, Silva, Araújo, & Torres, 2014). In Brazil, the sesame-growing area expanded from 53,000 ha in the 2018/2019 harvest to 175,000 ha in the 2019/2020 harvest, which represents a 230% increase. Production grew 123%, from 41,300 t to 95,800 Mg of grain (Empresa Brasileira de Pesquisa Agropecuária [EMBRAPA], 2022).

Sesame adapts well to the conditions found in the Brazilian semiarid region, tolerating low humidity and soil fertility. Its production is maximized under annual precipitation between 500 and 650 mm, a situation encountered in several areas of the semi-arid region of northeast Brazil (Arriel et al., 2006). The crop has great potential for exploitation that is within the reach of small- and medium-sized producers, as it requires simple and easy-to-assimilate agricultural practices. As such, it has an important socioeconomic function in generating income and employment for the semi-arid region of the Brazilian northeast (Guimarães et al., 2013; Nóbrega et al., 2018). This region faces limitations due to its physico-environmental characteristics, such as high temperatures, irregular distribution of rainfall, and intense evaporation (Souza, Nobre, Silva, Gheyi, & Soares, 2017; Bezerra et al., 2018a), which result in a negative water balance during most part of the year.

Successful agricultural production in this region depends on irrigation management, the plant's tolerance to salinity, and nutrient supply, considering that most of the water sources available in this region have high concentrations of soluble salts (Dias, Lima, Gheyi, Nobre, & Santos, 2017). The use of water with high concentrations of salts can inhibit plant growth and production, since high salt levels in the soil lead to a decrease in osmotic potentials, preventing the plant from absorbing water, which can result in a condition of physiological drought (A. A. R. da Silva et al., 2019a; Zahra, Raza, & Mahmood, 2020).

Excessive concentrations of Na+ and Cl- induce ionic toxicity, nutritional imbalances, or both simultaneously (Syvertsen & Garcia-Sanchez, 2014; Bezerra et al., 2018b). Additionally, they impact the absorption of essential nutrients such as K, Ca, Mg, and N (Abdallah et al., 2016) through competitive interactions that affect the ionic selectivity of cell membranes and photosynthetic activity, reducing stomatal opening and leading to a decrease in intracellular CO_2 (Gomes, Pestana, Santa-Catarina, Hauser-Davis, & Suzuki, 2017).

This stress also reduces the activity of the photosynthetic system due to the low production of photosynthetic pigments and stimulation of the synthesis of chlorophyllase, an enzyme that degrades chlorophyll molecules (F. I. F. de Oliveira et al., 2018). According to Melo, Souza and Cunha (2017), a high concentration of salts causes damage to the photosynthetic apparatus and the metabolic processes of plants, reducing the content of pigments that constitute the antenna complex and, consequently, the capture of light energy.

However, tolerance to salt stress varies with the botanical species, the concentration and ionic nature of the salts, exposure period, phenological stage, and availability of nutrients such as N, P, and K and their interaction (Sá et al., 2018). Thus, with proper irrigation management as well as agricultural practices such as mineral fertilization in these areas, satisfactory crop yields can be achieved, making these low-quality waters viable for agricultural systems.

According to F. R. A. de Oliveira, Oliveira, Medeiros, Sousa and Freire (2010), increasing P rates can minimize the adverse effects of salinity on plant development. For Diniz et al. (2018), the application of phosphorus plays a key role in photosynthesis. This nutrient is essential in the Calvin-Benson cycle for the formation of trioses-phosphate and, consequently, the synthesis of starch and sucrose for the formation of biomass and plant growth. In addition, P promotes root development, water use efficiency, and nutrient absorption and utilization.

Considering the foregoing, this study was developed to examine the effects of irrigation with saline water and different phosphorus fertilizer rates on the growth, gas exchange, photosynthetic pigments, and photochemical efficiency of sesame cv. BRS Seda.

Material and Methods

The experiment was conducted from April to August 2019, in a greenhouse belonging to the Center of Agri-Food Science and Technology at the Federal University of Campina Grande (CCTA/UFCG) in Pombal - PB, Brazil. According to the Köppen classification adapted for Brazil (Alvares, Stape, Sentelhas, Moraes, & Sparovek, 2013), the location has a climate classified as a BSh type, i.e., hot semi-arid, with average annual temperature of 28 °C, precipitation around 750 mm year^{-1}, and average annual evaporation of 2000 mm.

The experiment was laid out in a randomized-block design with three replicates in a 5 × 4 factorial arrangement whose treatments consisted of five levels of electrical conductivity of the irrigation water (ECw: 0.3 [control], 1.1, 1.9, 2.7, and 3.5 dS m^{-1}) and four phosphorus rates (40, 70, 100, and 130% of the rate recommended by Novais, Neves and Barros (1991) for pot trials). The P rate of 100% corresponded to 300 mg P_2O_5 kg^{-1} of soil. The ECw levels were established based on the study conducted by Lima, Lacerda, Soares, Gheyi and Araújo (2020a).

The crop evaluated in this study was sesame cv. BRS Seda. Plants were grown in sixty 20-L pots (35 cm height × 31 cm upper diameter × 20 cm lower diameter) that were adapted as drainage lysimeters, with a hose at the base for collecting the leachate in a container, aiming to determine water consumption by plants. The end of the drain inside the pot was covered with a non-woven geotextile (Bidim OP 30) to prevent obstruction by soil material. Each lysimeter was filled with a layer of 0.5 kg of screenings gravel (4.8 to 9.5 mm particles), followed by 23.5 kg of a Regosol (Psamments) of sandy clay loam texture from the rural area of São Domingos - PB, whose chemical and physical traits (Table 1) were determined as per Teixeira, Donagemma, Fontana and Teixeira (2017).

Table 1

Chemical and physical characteristics of the soil (0-0.40 m layer) used in pots for sesame growing in 2019, in Pombal - PB

Chemical characteristics								
pH (H_2O) (1:2.5)	OM g kg^{-1}	P (mg kg^{-1})	K^+	Na^+	Ca^{2+}	Mg^{2+}	Al^{3+}	H^+
			..........cmol$_c$ kg^{-1}..........					
5.58	2.93	39.2	0.23	1.64	9.07	2.78	0.0	8.61
..........Chemical characteristics..........				..........Physical characteristics..........				
EC_{se}	CEC	SAR_{se}	ESP	Particle size (g kg^{-1})			Moisture content (dag kg^{-1})	
(dS m^{-1})	cmol$_c$ kg^{-1}	(mmol L^{-1})$^{0.5}$		Sand	Silt	Clay	33.42 kPa^1	1519.5 kPa^2
2.15	22.33	0.67	7.34	572.7	100.7	326.6	25.91	12.96

pH - potential of hydrogen, OM - organic matter: Walkley-Black Wet Digestion; Ca^{2+} and Mg^{2+} extracted with 1M KCl pH 7.0; Na^+ and K^+ extracted using 1M NH_4OAc pH 7.0; Al^{3+} + H^+ extracted using 0.5M CaOAc pH 7.0; ECse - electrical conductivity of the saturation extract; CEC - cation-exchange capacity; SARse - sodium adsorption ratio of the saturation extract; ESP - exchangeable sodium percentage; 1.2 refering to field capacity and permanent wilting point.

The irrigation waters were prepared according to each electrical conductivity level by dissolving NaCl in supply water of the municipality of Pombal - PB, whose electrical conductivity during the research period was 0.3 dS m^{-1}. To prepare the ECw levels, the relation between ECw and salt concentration (Richards, 1954) was considered, according to Eq. 1:

$$A\ (mmol_c\ L^{-1}) = 10 \times ECw \ldots\ldots(1),$$

where A - amount of salts to be applied ($mmol_c$ L^{-1}); and ECw - electrical conductivity of water (dS m^{-1}).

Before sowing, the soil moisture content was raised to field capacity. Supply water was used in all treatments for a period of 20 days for the establishment of the crop. After its establishment, the plants were irrigated daily with saline water according to each treatment, applying the volume corresponding to that obtained by the water balance in each lysimeter, as determined by Eq. 2:

$$Vi = \frac{(Vp - Vd)}{(1 - LF)} \ldots\ldots(2),$$

where Vi - volume of water to be applied (mL); Vp - volume applied in the previous irrigation event (mL); Vd - drained volume (mL); and LF - leaching fraction of 0.1.

Topdressing with nitrogen (25 mg N kg^{-1} of soil) and potassium (37.5 mg K_2O kg^{-1} of soil) was performed at 10, 20, 30, and 40 days after sowing (DAS). Phosphate fertilization was applied according to each treatment, using 1/3 of the recommended rate at establishment. The remaining 2/3 were divided into two applications, at 10 and 20 DAS. Urea, monoammonium phosphate (MAP), and potassium chloride (KCl) were used as the sources of N + P, and K, respectively. Micronutrient fertilization was carried out weekly by foliar spray, using solution (1.0 g L^{-1}) of Ubyfol® (15% N, 15% P_2O_5, 15% K_2O, 1% Ca, 1.4% Mg, 2.7% S, 0.5% Zn, 0.05% B, 0.5% Fe, 0.05% Mn, 0.5% Cu, and 0.02% Mo).

Vegetative development was evaluated 60 DAS by measuring the variables of stem diameter (SD, mm) and plant height (PH, cm). Chloroplast pigments were quantified based on the contents of chlorophylls *a* (Chl *a*) and *b* (Chl *b*) and carotenoids. Gas exchange was evaluated based on stomatal conductance (*gs*, mol H_2O m^{-2} s^{-1}), transpiration (*E*, mmol H_2O m^{-2} s^{-1}), CO_2 assimilation rate (*A*, μmol CO_2 m^{-2} s^{-1}), intercellular CO_2 concentration (*Ci*, μmol CO_2 m^{-2} s^{-1}), and instantaneous carboxylation efficiency (*CEi*, μmol m^{-2} s^{-1} (μmol m^{-2} s^{-1})$^{-1}$).

Plant height was measured as the distance from the plant neck to the insertion of the apical meristem, whereas SD was measured at 2 cm from the plant neck. Chlorophyll and carotenoid contents were quantified with a spectrophotometer at the absorbance wavelengths (ABS) of 470, 646, and 663 nm, according to the method proposed by Arnon (1949), using Eqs. 3, 4, and 5:

$$\text{Chl } a = 12.21\ ABS_{663} - 2.81\ ABS_{646} \ldots\ldots(3)$$

$$\text{Chl } b = 20.13\ ABS_{646} - 5.03\ ABS_{663} \ldots\ldots(4)$$

$$\text{Car} = (1000\ ABS_{470} - 1.82\ \text{Cl } a - 85.02\ \text{Cl } b)/198 \ldots\ldots(5),$$

where Chl *a* - chlorophyll a; Chl *b* - chlorophyll *b*; and Car - total carotenoids. The chlorophyll *a* and *b* and carotenoid values recorded in the leaves were expressed in mg g^{-1} of fresh weight (FW).

Gas exchange was measured using a LCpro - SD infrared gas analyzer (IRGA; ADC Bioscientific, UK), on the fully expanded middle leaf of the productive branch. Readings were taken between 07h00 and 10h00, under natural conditions of air temperature and CO_2 concentration, and using an artificial radiation source of 1200 µmol m^{-2} s^{-1}, determined by the photosynthetic light saturation curve (Fernandes et al., 2021).

On the same day, chlorophyll a fluorescence was determined using a pulse modulated fluorometer to determine the initial (F_0), maximum (*Fm*), and variable ($Fv = Fm – F_0$) fluorescence and quantum efficiency of photosystem II (*Fv/Fm*). Readings were taken after adapting the middle leaves of the productive branch to the dark, using leaf tweezers to ensure that all acceptors were oxidized, that is, with the reaction centers open for 30 min, using a PEA II® (Modulated Plant Efficiency Analyzer) fluorometer.

Data were subjected to the Shapiro-Wilk normality test, followed by analysis of variance, using the F test. For cases in which the F test was significant, polygonal regression analyses were conducted for the 'water salinity level' and 'phosphorus rate' factors using SISVAR 4.2 SISVAR-ESAL statistical software (D. F. Ferreira, 2014).

Results and Discussion

There was a significant interaction effect between water salinity levels and P rates on the contents of chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), and carotenoids (Table 2). Water salinity levels significantly influenced plant height (PH), stem diameter (SD), Chl *a*, Chl *b*, carotenoids, stomatal conductance (*gs*), CO_2 assimilation rate (*A*), transpiration (*E*), and initial fluorescence (F_0), whereas the P rates significantly affected PH, Chl *a*, Chl *b*, Car, *gs, A,* instantaneous carboxylation efficiency (*CEi*), variable fluorescence (*Fv*), maximum fluorescence (*Fm*), and quantum efficiency of photosystem II (*Fv/Fm*) (Table 2).

Water salinity negatively affected the height of the sesame plants (Figure 1A), which decreased linearly by 3.68% with each unit increase in ECw, corresponding to a reduction of 11.89% between plants irrigated with 3.5 dS m^{-1} and those subjected to the lowest salt level (0.3 dS m^{-1}). Stem diameter (Figure 1B) showed the same trend as PH, with a reduction of 5.57% per unit increase in water salinity. When we compare the SD of plants subjected to 3.5 dS m^{-1} salinity and those irrigated with water with ECw of 0.3 dS m^{-1}, a reduction of 4.3 mm is observed.

Table 2
Summary of the F test for growth, gas exchange, photosynthetic pigments, and photochemical efficiency of sesame cv. BRS Seda irrigated with saline water and fertilized with phosphorus, at 60 days after sowing

Source of variation	Significance of the ‘F’ test						
	PH	SD	*Chl a*	*Chl b*	*Car*	*gs*	*A*
Electrical conductivity (ECw)	*	**	**	**	*	*	*
Linear regression	**	**	**	**	*	*	*
Quadratic regression	*	ns	**	**	*	*	ns
Phosphorus rate (PR)	*	ns	**	**	**	*	*
Linear regression	*	ns	**	**	**	ns	*
Quadratic regression	*	ns	ns	ns	ns	*	*
Interaction (ECw× PR)	ns	ns	**	**	**	ns	ns
Block	ns	ns	ns	ns	ns	ns	ns
CV (%)	11.12	9.10	19.26	33.75	24.41	31.90	40.47
	E	*Ci*	*CEi*	*F0*	*Fm*	*Fv*	*Fv/Fm*
Electrical conductivity (ECw)	*	ns	ns	*	ns	ns	ns
Linear regression	ns	ns	*	*	ns	ns	*
Quadratic regression	*	ns	ns	ns	ns	ns	ns
Phosphorus rate (PR)	ns	ns	*	ns	*	*	*
Linear regression	ns	ns	ns	ns	*	*	ns
Quadratic regression	*	ns	*	ns	*	*	*
Interaction (ECw× PR)	ns	ns	ns	ns	ns	ns	ns
Block	ns	*	ns	ns	ns	ns	ns
CV (%)	29.11	26.25	61.58	10.84	12.26	16.49	5.17

ns, *, ** correspond to non-significant and significant at $p<0.05$ and $p<0.01$, respectively; CV = coefficient of variation; PH = plant height; SD = stem diameter; Chl *a* = chlorophyll *a* content; Chl *b* = chlorophyll *b* content; Car = carotenoids; *gs* = stomatal conductance; *A* = CO_2 assimilation rate; *E* = transpiration; *Ci* = intercellular CO_2 concentration; *CEi* = instantaneous carboxylation efficiency; F_0, *Fm*, and *Fv* - initial, maximum, and variable fluorescence; and *Fv/Fm* - quantum efficiency of photosystem II.

Reduced growth is one of the first effects of salinity, which is a result of the inhibition of cell expansion caused by the decreased water absorption as well as the toxicity effect of the ions that were absorbed and are accumulated in the protoplasm (E. C. A. da Silva et al., 2019b). The reduction in water and nutrient absorption impairs several physiological processes in plants, including the photosynthetic process. And this set of consequences caused by salt stress results in growth inhibition and loss of productive potential in plants (Lima, Dias, Gheyi, Soares, & Andrade, 2018).

Phosphorus rates linearly reduced the height of the sesame plants (Figure 1C), which declined by 2.35% at each 30% increase in P rate. In plants fertilized with 130% of the recommended rate, an average reduction of 9.03 cm (7.26%) was observed in PH, relative to those that received 40% of the recommended rate. Araújo et al. (2014) found increases in the height of sesame plants in response to P rates from 0 to 120 mg L^{-1} in nutrient solution, which averaged 0.22 cm for each 1.0 mg L^{-1} of P applied. This is because P is an integral part of the ATP molecule, a compound that releases energy for the active process of nitrogen absorption (Taiz, Zeiger, Møller, & Murphy, 2017). Furthermore, the efficiency of the nitrogen fixation process is dependent on the availability of P, due to its participation in the symbiotic process (Bonfim-Silva, Oliveira, Anicesio, & Silva, 2016).

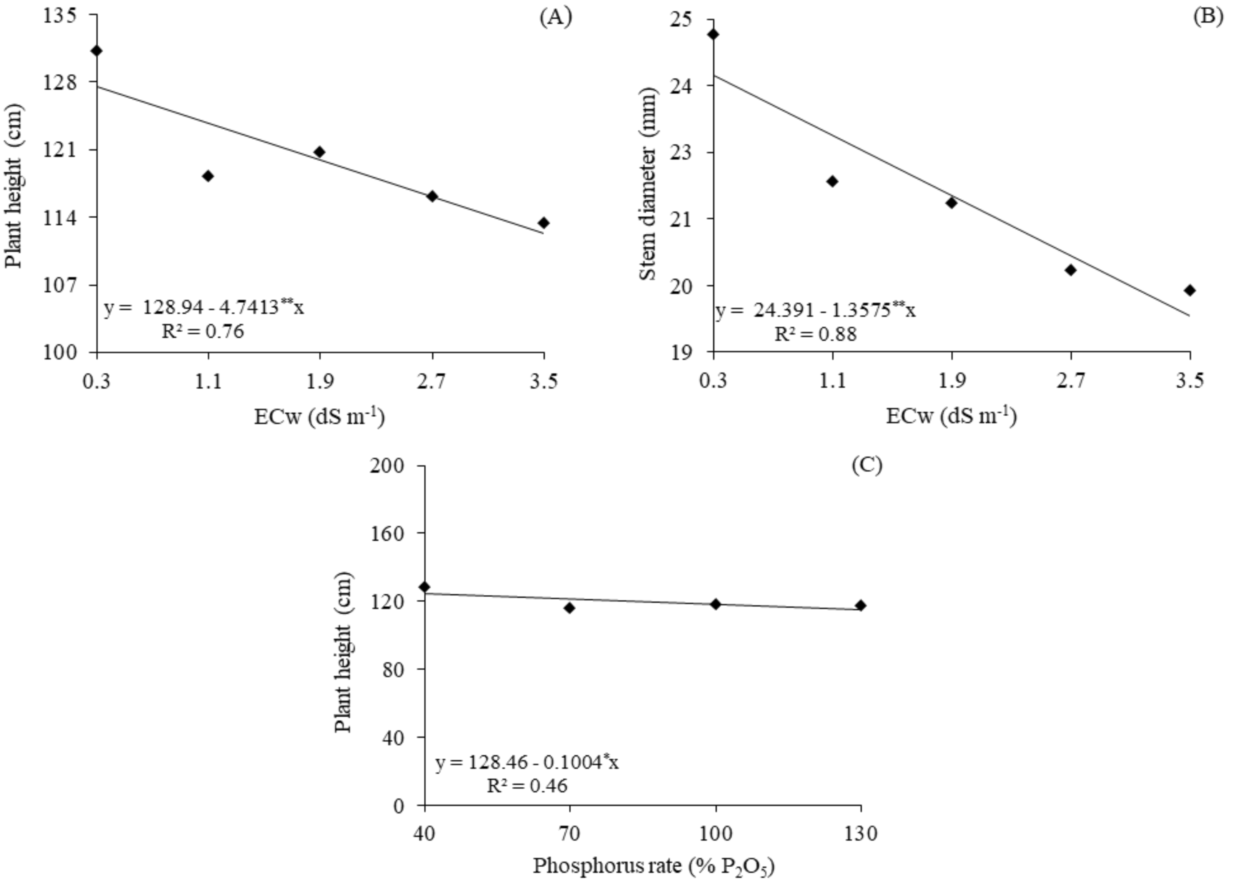

Figure 1. Plant height (A) and stem diameter (B) as a function of electrical conductivity (ECw) of irrigation water and height of sesame cv. BRS Seda as a function of phosphorus rates (C), at 60 days after sowing, in 2019, in Pombal - PB.

The divergence between the present study and that of Araújo et al. (2014) may be related to the conditions in which the crop was developed, since the above-mentioned study was conducted in nutrient solution, which reduces the matrix effect on total water availability. Mishra, Debnath and Rawat (2017), on the other hand, reported that depending on the ion concentration and pH of the soil, soil P is often associated with Fe^{2+} and Al^{3+}, in the case of acidic soils, or with Ca^{2+} in calcareous soil conditions, making it little available to plant roots.

As regards the chlorophyll a contents (Figure 2A), plants grown under electrical conductivity of 0.3 dS m^{-1} and fertilized at 130% of the level recommended by Novais et al. (1991) stood out with the maximum Chl a value of 1.29 mg g^{-1} FW. However, plants under irrigation with 3.5 dS m^{-1} water and fertilized with 40% P_2O_5 obtained a minimum Chl *a* value of 0.57 mg g^{-1} FW. Similar to what was observed for Chl a (Figure 2A), the water salinity of 0.3 dS m^{-1} and fertilization with a P_2O_5 rate of 130% provided the maximum Chl b value of 0.97 mg g^{-1} FW (Figure 2B) in the sesame plants. On the other hand, the minimum value of 0.23 mg g^{-1} FW was observed in plants cultivated under ECw of 3.5 dS m^{-1} and at the lowest P rate (40% P_2O_5). Thus, it can be inferred that the increase in phosphate fertilization is efficient in mitigating salt stress in sesame plants, due to its essential role in the photosynthetic apparatus through the action of the enzyme ribulose-1,5-bisphosphate carboxylase-oxygenase. The increase in the content of these pigments in response to the supply of phosphate fertilizer is also due to the greater absorption of nitrogen by the plant in the presence of P (Haim, Zoffoli, Zonta, & Araújo, 2012).

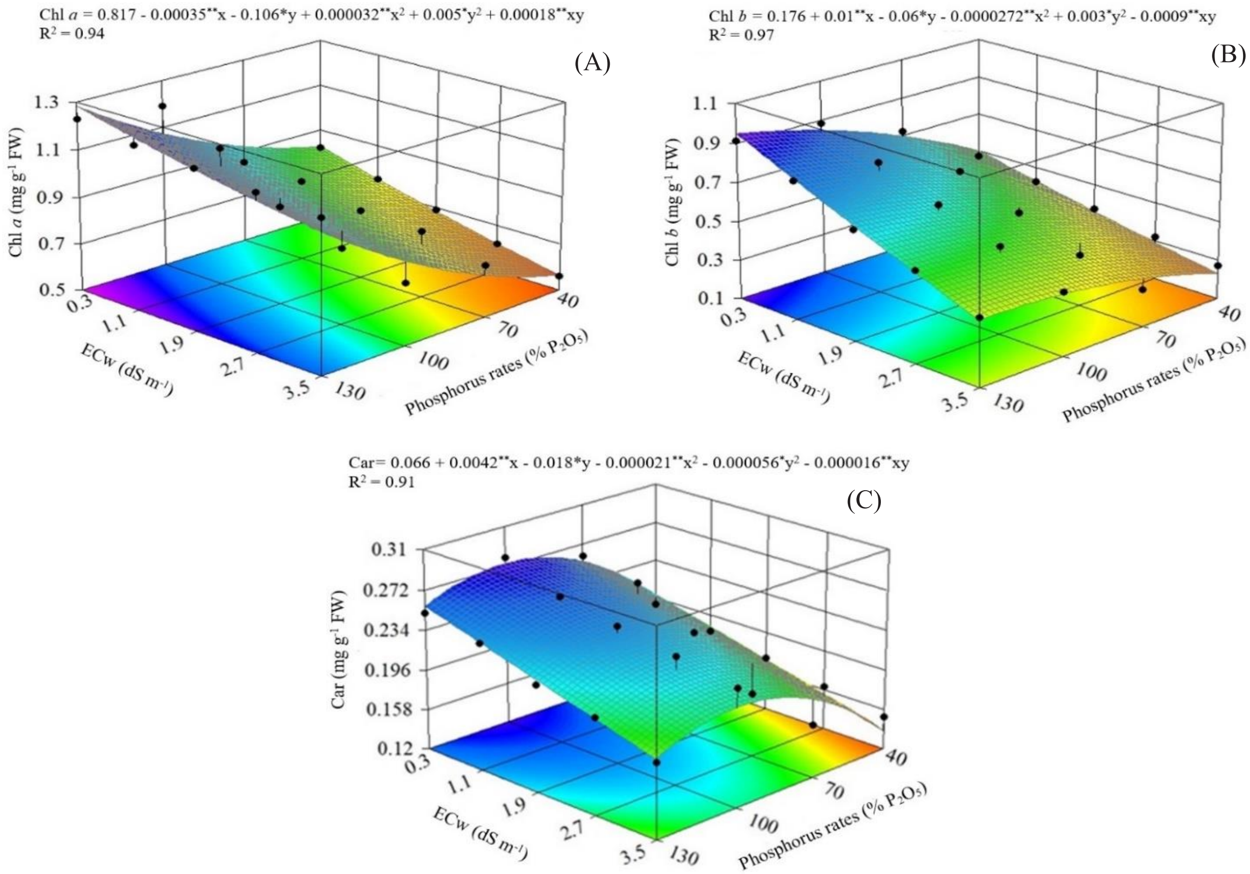

Figure 2. Chlorophyll *a* (Chl *a;* A), chlorophyll *b* (Chl *b;* B), and carotenoid (Car; C) contents of sesame cv. BRS Seda as a function of the interaction between water salinity levels (ECw) and phosphorus rates, at 60 days after sowing, in 2019, in Pombal - PB. X and Y correspond to ECw and phosphorus rates. * and ** represent significance at the 0.05 and 0.01 probability levels, respectively.

The sesame plants under electrical conductivity of 0.3 dS m^{-1} and fertilized with 100% P_2O_5 achieved the highest carotenoid synthesis (0.274 mg g^{-1} FW) (Figure 2C). The water salinity of 3.5 dS m^{-1} and fertilization with 40% P_2O_5 provided a decrease in carotenoid contents, with a minimum value of 0.134 mg g^{-1} FW. Carotenoids exert a photoprotective action on the photochemical apparatus by sequestering singlet oxygen ($^1O_2$) produced in the thylakoid membranes in PSII and acting as a filter of visible and UV light and contributing to preventing cell damage caused by excess radiation (Barbosa, Silva, Willadino, Ulisses, & Camara, 2014). Thus, the decrease in carotenoid levels may be related to the generation of reactive oxygen species (ROS), which impair plant metabolism by inducing the oxidation of photosynthetic pigments (A. R. A. da Silva, Bezerra, Lacerda, Sousa, & Chagas, 2016), among other reasons, in addition to causing degradation of beta-carotene, thereby reducing the content of carotenoids (Sousa, Gheyi, Brito, Silva, & Lima, 2017), recognized antioxidant metabolites.

According to the regression equation (Figure 3A), the stomatal conductance of the sesame plants showed a quadratic response to the increasing ECw. The maximum estimated value (0.1249 mol H_2O m^{-2} s^{-1}) was obtained in plants subjected to irrigation with water of 0.3 dS m^{-1} salinity, and the lowest (0.1138 H_2O m^{-2} s^{-1}) at the ECw level of 2.2 dS m^{-1}. Plants subjected to salinity have their osmotic potential reduced, which makes it difficult for the roots to absorb water and nutrients, inducing the plant to reduce stomatal opening as a primary mechanism. Consequently, there is a discrepancy between water absorption by the roots and transpiration; however, the partial closure of the stomata is considered a strategy to avoid excessive dehydration or an effect of water imbalance in the epidermis of the leaves, a mechanism that leads to decreased growth and production with increasing severity of stress (Machado, Machado, Machado, & Ribeiro, 2010).

Like *gs,* transpiration (Figure 3B) also responded quadratically to the increase in ECw, with the highest estimated value (2.9078 mmol H_2O m^{-2} s^{-1}) obtained when the plants were subjected to the highest ECw level (3.5 dS m^{-1}), and the minimum (2.5817 mmol H_2O m^{-2} s^{-1}) at the ECw level of 1.7 dS m^{-1}. It is noteworthy that irrigation with intermediate saline levels caused the E of the sesame plants to decrease when compared with the plants irrigated with the lowest salinity level (0.3 dS m^{-1}). The CO_2 assimilation rate of the sesame plants was negatively affected by increasing water salinity levels. According to the regression equation (Figure 3C), there was a linear decrease of 7.82% in *A* per unit increase in ECw, corresponding to a reduction of 2.69 μmol m^{-2} s^{-1} in the A of plants under the highest salinity in comparison to those cultivated under an ECw of 0.3 dS m^{-1}.

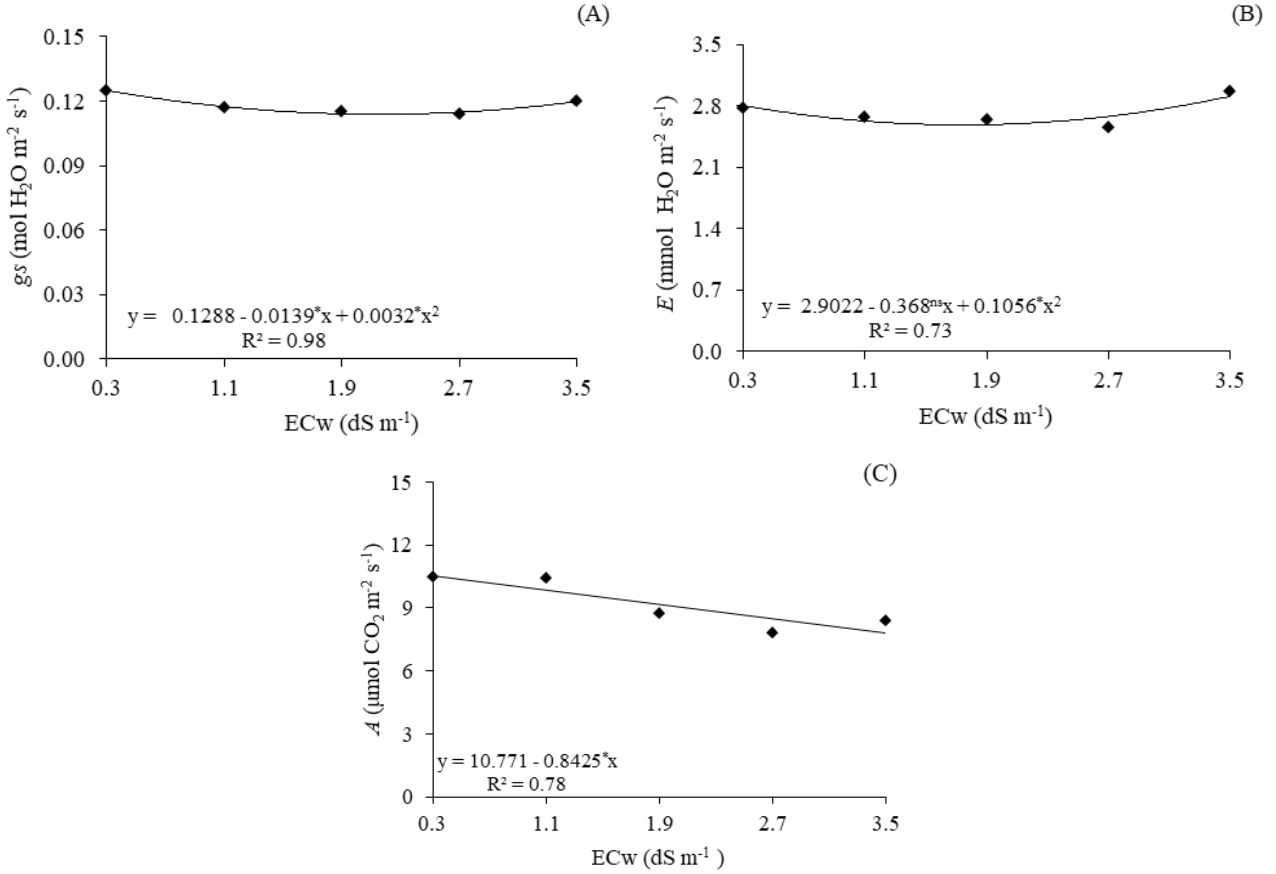

Figure 3. Stomatal conductance (*gs*; A), transpiration (*E*; B), and CO_2 assimilation rate (*A*; C) of sesame cv. BRS Seda as a function of irrigation water salinity (ECw), at 60 days after sowing, in 2019, in Pombal - PB.

The decrease in *A* is in line with the reductions observed in *gs* and *E* (Figure 3A and 3B, respectively), which limit the amount of water absorbed as well as CO_2 fixed by the plant, resulting in less substrate for the photosynthetic process. However, the limitation in the photosynthetic process of sesame also occurs in response to the reduction in chlorophyll contents caused by the increase in ECw (Figure 2), which are key molecules in this process.

Agreeing with the above descriptions, Ouzounidou, Giannakoula and Zamanidis (2016) stated that the decreased plant photosynthesis caused by increased salinity may be due to several factors, e.g., stomatal closure, which induces a reduction in stomatal conductance, in *Ci,* and in chlorophyll levels, suggesting damage to the photosynthetic apparatus and resulting in reduced efficiency of the photosensitive system and other specific metabolic factors in carbon assimilation.

Regarding the effects of P rates on stomatal conductance (Figure 4A), the data fitted the quadratic model, which revealed that the minimum value of *gs* (0.095 mol H_2O m^{-2} s^{-1}) was obtained under 90% of the recommended P rate, with a subsequent increase from this point, culminating at 0.111 mol H_2O m^{-2} s^{-1} under 130% of the recommended value. Phosphorus is an essential element in plant metabolism; plays an important role in respiration, storage, transport, and use of energy in the photosynthetic process; and also acts in protein synthesis and enzyme metabolism (Rocha, 2018).

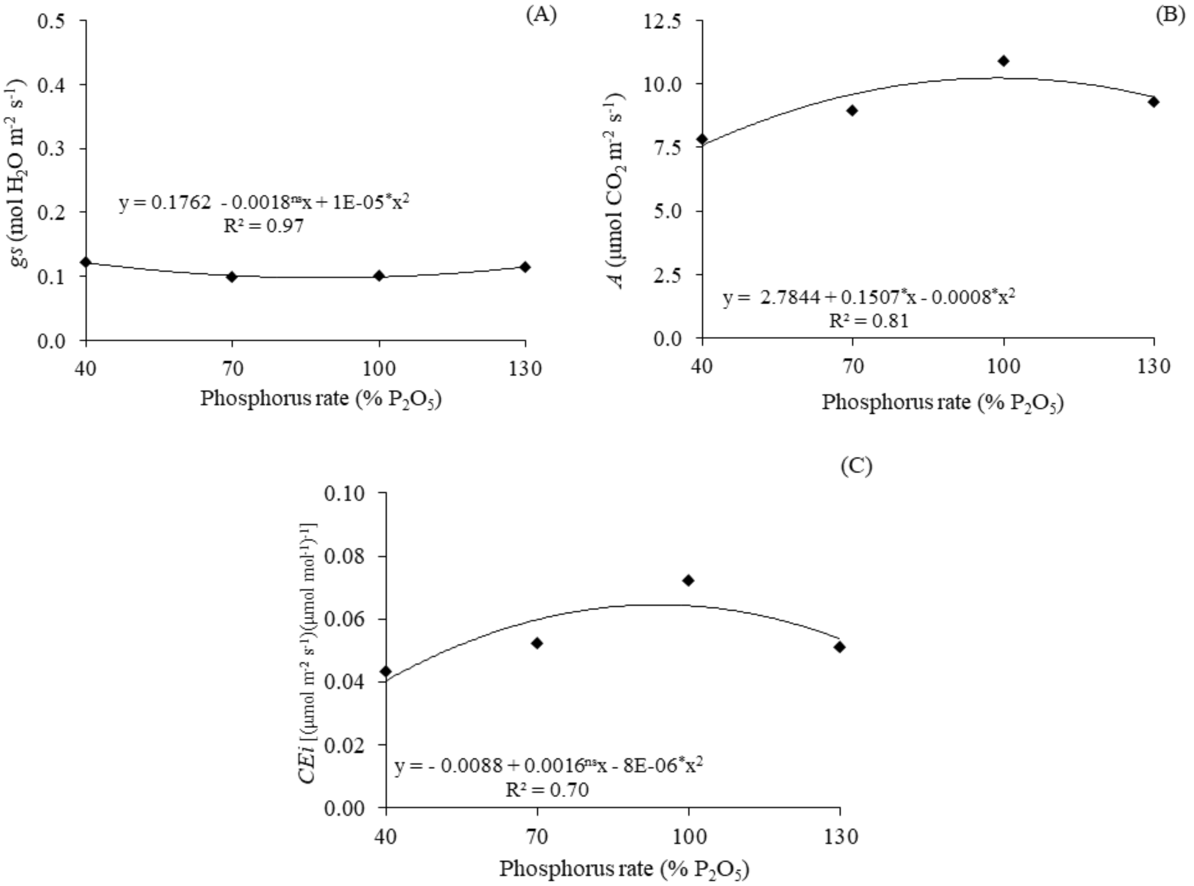

Figure 4. Stomatal conductance (*gs*; A), CO_2 assimilation rate (*A*; B), and instantaneous carboxylation efficiency (*CEi*; C) of sesame cv. BRS Seda as a function of increasing phosphorus rates (C), at 60 days after sowing, in 2019, in Pombal - PB.

The CO_2 assimilation rate showed a quadratic response to increasing P rates (Figure 4B), with the highest value (9.8544 µmol CO_2 m^{-2} s^{-1}) found in plants fertilized with 100% of the recommended P rate. Instantaneous carboxylation efficiency also responded quadratically to increasing P rates, showing better performance [0.0712 (µmol m^{-2} s^{-1})(µmol mol^{-1})$^{-1}$] at the recommended P rate (100%) and declining thereafter (Figure 4C). The supply of P constitutes an auxiliary tool in the management of plants under salt stress, given that the increased synthesis of chloroplast pigments and gas exchange under these conditions mitigated the deleterious effects of this stress on the photosynthetic apparatus of the sesame crop.

This situation can be attributed to the action of P in several processes of photosynthetic activity, e.g., participating in photosynthetic pathways (C3, C4) and glycolysis, in addition to exerting a structural function in macromolecules such as adenosine triphosphate (ATP), phospholipids, and nucleic acids (L. da Silva et al., 2010). This element is also involved in stomatal opening, the main influencer of gas exchange, improving transpiration, water flow, and CO_2 diffusion (Lima et al., 2020b) and thus stimulating *A* and *CEi.*

Increasing irrigation water salinity affected the initial fluorescence of sesame cv. BRS Seda at 60 DAS, which increased by 2.0% with each unit increase in ECw, i.e., 6.36% increase in F_0 in the plants irrigated with 3.5 dS m^{-1} relative to those under 0.3 dS m^{-1} (Figure 5A). The increase in F_0 indicates damage and inactivation of the reaction centers of the PSII light-harvesting complex (Mehta, Jajoo, Mathur, & Bharti, 2010) or a decrease in the ability of the PSII antenna complex to transfer excitation energy (Andrade et al., 2019).

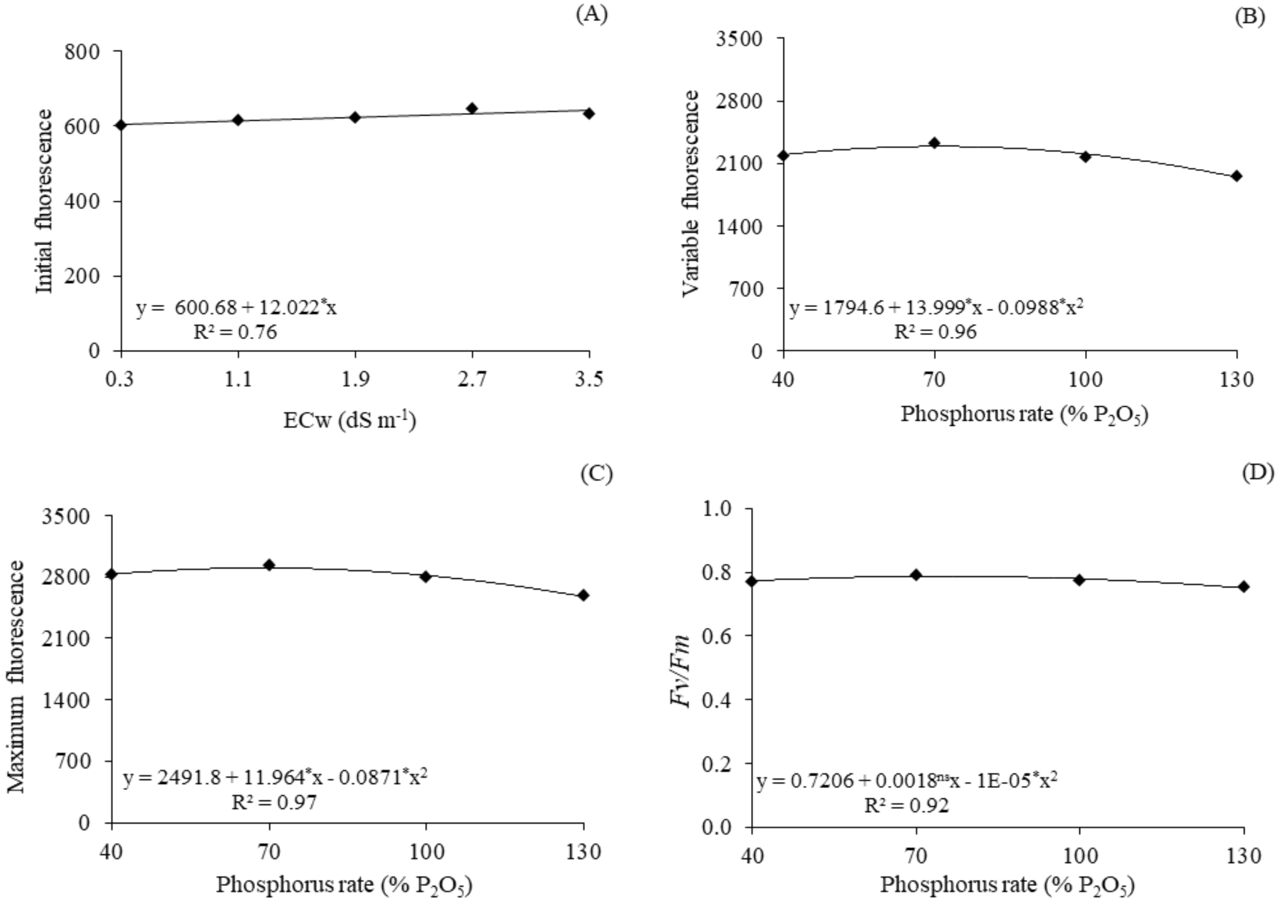

Figure 5. Initial fluorescence (A) as a function of the electrical conductivity of irrigation water (ECw) and variable fluorescence (B), maximum fluorescence (C), and quantum efficiency of photosystem II (*Fv/Fm*; D) of sesame cv. BRS Seda as a function of phosphorus rates at 60 days after sowing, in 2019, in Pombal - PB.

These results indicate a greater loss of energy by the chlorophyll complex, which may be related to the greater difficulty of plants in absorbing water and optimizing the process of free energy consumption (F. N. Ferreira et al., 2021). In line with this study, Andrade et al. (2019) evaluated the tolerance of cowpea (*Vigna unguiculata* L. Walp.) genotypes to salt stress, through chlorophyll fluorescence analysis, and also observed an increase in initial fluorescence in common-bean genotypes MNCO3-737F-5-9, MNCO2-676F-3, BRS Marataoã, and Pingo de Ouro, respectively, when the plants were subjected to an ECw of 5.1 dS m^{-1}, indicating sensitivity to salt stress.

Increasing P rates affected the variable (Figure 5B) and maximum (Figure 5C) fluorescence of sesame, whose highest values (*Fv* = 2290.47 and *Fm* = 2902.63) values were achieved at 71 and 69% of the recommended P rate, respectively. Variable fluorescence represents the potentially active energy in PSII, and is directly influenced by *Fm*, both of which showed a quadratic response to phosphate fertilization. Maximum fluorescence, on the other hand, represents the maximum intensity of fluorescence, when practically all the quinone is reduced by the electrons transferred from P_{680} and the PSII reaction centers reach their maximum capacity for photochemical reactions. This influences the plant's ability to transfer energy for the formation of the reductant NADPH, ATP, and the reduced ferredoxin, consequently affecting CO_2 assimilation in the biochemical phase of photosynthesis (Dias et al., 2021).

Overall, it can be stated that the fluorescence signals of chlorophyll *a* are used to measure the efficiency of the photochemical reactions of photosynthesis, and that these variables can be affected by abiotic factors (Dias, Lima, Pinheiro, Gheyi, & Soares, 2019). Furthermore, changes in *Fv* and *Fm* indicate possible damage to the PSII light-harvesting complex. The *Fv/Fm* ratio showed a quadratic behavior, with a maximum point (0.802) reached at 88% of the recommended P rate, which represents an increase of 3.11% relative to that seen in plants subjected to 40% of the recommended rate (Figure 5D). There are reports that plants under no stress show quantum efficiency of photosystem II (*Fv/Fm*) in the range of 0.75 to 0.85 and that *Fv/Fm* values below or above this range reflect photoinhibitory damage to the reaction centers of photosystem II (Cruz, Cruz, Ferreira, Castro, & Almeida, 2014; Freire, Dias, Cavalcante, Fernandes, & Lima, 2014; Sousa et al., 2016; Guidi, Lo Piccolo, & Landi, 2019). Although the lowest value for Fv/Fm (0.776) was obtained in plants grown under 40% P_2O_5 (Figure 5D), it must be considered that there was no photochemical damage, as it is within the range established by the above-mentioned authors.

Conclusions

Water salinity levels above 0.3 dS m^{-1} reduce the growth, chloroplast pigment levels, and gas exchange of sesame cv. BRS Seda.

Applying 100 and 130% of the recommended phosphorus rate minimizes the effects of salt stress on the CO_2 assimilation rate and photosynthetic pigment synthesis of sesame cv. BRS Seda.

The increase from 40 to 130% of the recommended phosphorus rate does not change the photochemical efficiency of sesame cv. BRS Seda at 60 days after sowing.

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