Gas exchanges in sugar apple (*Annona squamosa* L.) subjected to salinity stress and nitrogen fertilization

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Abstract

Salinity is one of the modern agriculture major obstacles, causing several physiological disturbances in plants, adversely affecting its growth and development. Therefore, some techniques are required in order to alleviate the negative effects of salinity stress on plants, as for example an adequate nitrogen fertilization. The aim of this study was to assess the ecophysiological responses of sugar apple plants (*Annona squamosa* L.) submitted to different salinity levels and nitrogen fertilization doses. The experimental design was a randomized block in an incomplete factorial scheme, with five electrical conductivities of the irrigation water (EC_w: 0.5, 1.01, 2.25, 3.49 and 4.0 dS m^{-1}) and five nitrogen doses (0, 101, 350, 598.2 and 700 mg dm^{-3}), with four replicates, generated from the Box Central Composite experimental design matrix. Through a daily course, it was observed variations in gas exchange, chlorophyll content and fluorescence parameters. The gas exchange, chlorophyll content and fluorescence parameters were measured on photosynthetically active leaves. There was significant interaction between the salinity levels (EC_w) and nitrogen doses for the chlorophyll indexes. The electrical conductivity of the irrigation water caused significant negative effects on chlorophyll fluorescence. Therefore, it can be stated that the sugar apple plants ecophysiology varies through the day and that salinity affects its chlorophyll content and fluorescence.

Keywords: *Annona squamosa* L.; photosynthetic daily course and ecophysiology.
Abbreviations: EC_w_ electrical conductivity of the irrigation water, DAS_30 days after sowing, : *A*_net CO_2 assimilation rate, *gs*_ stomatal conductance, *Ci*_ intercellular CO_2 concentration, *E*_ transpiration rate, VPD_vapor pressure deficit, WUE_ water-use efficiency, iWUE_ intrinsic water-use efficiency, iCE_ instantaneous carboxylation efficiency, F_0_ initial fluorescence, F_m_ maximum fluorescence, F_v_ variable fluorescence and F_v/F_m_ quantum yield of photosystem II.

Introduction

The world's population is increasing rapidly, as is the global food demand, which brings a challenge to the food supply chain, especially to the agricultural sector. The situation becomes more challenging due to quality-water scarcity, especially in arid and semiarid regions, where irrigation with high salinity waters limits agricultural production and yield (Dias et al., 2016).

High salt concentrations in the irrigation water and soil cause a series of stresses in the plant, such as nutritional imbalance due to the accumulation of sodium, chlorine and sulfates inside the plant tissues, which reduces some essential nutrients absorption like nitrogen, phosphorus, calcium and potassium. In addition, the plants water absorption capacity is reduced due to decreased osmotic potential (Parihar et al., 2014).

Plant metabolic activity rates are influenced by both biotic and abiotic factors (Baron et al., 2014). Sugar apple plants (*Annona squamosa* L.) under high salt concentrations have their gas exchanges and chlorophyll fluorescence reduced, which reveals the species sensitiveness to salinity stress (Marler and Zozor, 1996; Sá et al., 2015).

Sugar apple, also known as sweetsop or pinha, is the fruit of *Annona squamosa*, a tree native to the Antilles and South America that is cultivated in tropical regions around the world. A. *squamosa* is a small evergreen tree from the family Annonaceae. The sugar apple, as a tropical fruit, presents

several beneficial effects on human health and it is traditionally used for treatments of dysentery, heart problems, fainting, worm infections, constipation, hemorrhage, fever, malignant tumors and ulcers. Besides being highly appreciated *in natura*, the sugar apple fruit is also used to make juices, ice creams and milkshakes, due to its creamy white pulp, which has high nutritional value in the food industry (Tu et al., 2016).

Bezerra et al. (2014) state that nutritionally balanced plants have greater resistance to environmental stresses, thus an adequate fertilization is needed in order to improve plant resistance against stress conditions. In this sense, nitrogen is one of the most required essential nutrient, due to its several functions on plant metabolism, being an important component of chlorophyll, amino acids and proteins (Veloso et al., 2018). When an adequate amount of nitrogen is supplied, the plant photosynthetic capacity is stimulated, due to an increase in stromal proteins and thylakoids in leaf chloroplasts (Akram et al., 2011).

The nitrogen fertilization can attenuate the effects of salinity stress on plants through the interaction between salinity and nutrition. With this, plant growth is stimulated due to the sufficient absorption of nitrogen at different phenological phases (Oliveira et al., 2018). However, excess N fertilization may contribute to soil salinization and increase the negative effects of soil salinity on plant growth and development (Chen et al., 2010).

Some studies were carried out aiming to evaluate the effects of nitrogen fertilization on the production of seedlings under salinity stress. Among these, we can highlight the studies carried out with jackfruit (*Artocarpus heterophyllus* L. - Oliveira et al., 2017; Oliveira et al., 2018), cotton (*Gossypium hirsutum* L. – Chen et., 2010), sugar cane (*Saccharum* sp. – Nadian et al., 2012), maize (*Zea mays* L. – Akram et al., 2011), wheat (*Triticum aestivum* L. – Elgharably et al., 2010) and sunflower (*Helianthus annuus* L. – Santos et al., 2016). Therefore, the aim of this study was to evaluate the ecophysiological responses of *Annona squamosa* L. submitted to different salinity levels and nitrogen doses.

Results and Discussion

Chlorophyll index

In higher plants, the photoassimilates originated from the leaves generates the motive power for the sink organs metabolism, which supports the plants growth and development (Bhatnagar and Singh, 2013). Diurnal variation in chlorophyll content is shown in Figure 1. It was noted that there were statistical differences for the chlorophyll *a* and *total* indexes.

Results obtained for chlorophyll *a* and *total* indexes showed gradual increase up to 1:00 p.m. (Fig 1A and 1C, respectively). However, from 1:00 p.m. on, the content of chlorophyll *a* and *total* started to decrease. It was also observed that the results obtained in the last assessment time (5:00 p.m.) and at 9:00 a.m. were similar. Regarding the chlorophyll *b*, its values increased up to 11:00 a.m. and decreased up to 1.5% when compared to the values obtained at 1:00 p.m. This observation may be related to the higher chlorophyll production under greater luminosity incidence periods, in order to absorb larger amounts of solar radiation.

There was significant interaction between the EC_w and nitrogen doses for the chlorophyll indexes (Fig 2). The presence of salts in the soil solution, due to the irrigation with saline water, may favor increased chlorophyll content in salt-tolerant plants and decreased in more susceptible plants. The chlorophyll index reduction may be associated to reactive oxygen species formation and/or to the photoinhibition of photosynthesis (Heidari, 2012). *A. squamosa* plants are sensitive to salinity stress in its initial growth stage (Marler and Zozor, 1996; Passos et al., 2005).

Sugar-apple plants presented higher chlorophyll indexes when fertilized with 101 mg dm^{-3} of nitrogen, at 0.5 dS m^{-1} salinity level (Fig 2A). The highest chlorophyll *b* values were observed up to the salinity level of 1.01 dS m^{-1} and 350 mg dm^{-3} of nitrogen (Fig 2B). The highest *total* chlorophyll values were observed in plants submitted to, approximately, 101 mg dm^{-3} of nitrogen and at the salinity level of 1.01 dS m^{-1} (Fig 2C). Increasing levels of salinity (EC_w) and nitrogen doses led to decreased chlorophyll indexes, thus indicating an increase in ions toxicity with the increase of nitrogen fertilization. The lowest chlorophyll indexes values were observed at 4.0 dS m^{-1} salinity level. Depressed photosynthetic rates observed in plants under salinity stress is not due to photosynthetic apparatus damage, but rather to low CO_2 availability resulted from reduced stomatal conductance (Tarchoune et al., 2012).

Chlorophyll fluorescence

Chlorophyll fluorescence and quantum yield of PSII are shown in Figure 3. Such variables may be a subtle reflection of the primary reactions of photosynthesis, being the relationship between fluorescence kinetics and photosynthesis a key to understanding the photosynthetic biophysical processes (Shu et al., 2013).

The initial fluorescence (F_0) increased until 1:00 p.m., when the highest mean value (97.56 electrons quantum^{-1}) was observed. At 3:00 p.m. a decrease was verified, increasing again (10.6%) at 5:00 p.m. (Fig 3A). The highest maximum fluorescence (F_m) was observed at 7:00 p.m., with 351.28 quantum^{-1} electrons. The other assessment times presented oscillations (Fig 3B). The same behavior was observed for the variable fluorescence (F_v) (Fig 3C). The quantum yield of PSII (F_v/F_m) decreased until 1:00 p.m., then its values started to increase and were close to those found at 7:00 p.m. (Fig 3D). According to Baron et al. (2014), the temperature of the roots is a factor that influences the Annonaceae plants, which may lead to the reduction of photosynthesis and phytomass production. This may be one of the factors that influenced the quantum yield of PSII, since during the highest temperature, at 1:00 p.m., F_v/F_m presented the lowest mean value (0.71).

Regarding the EC_w, there were oscillations in the chlorophyll fluorescence variables (Fig 4). Chlorophyll fluorescence analysis can provide useful information about the state of the plant, besides offering a cause-effect relationship between the mechanisms controlling water balance and plant growth (Mancarella et al., 2016).

The initial fluorescence (F_0) increased up to the EC_w of 2.25 dS m^{-1}, then it started to decrease in the following salinity levels (Fig 4A). The maximum fluorescence (F_m) showed the highest mean value (331 electrons quantum^{-1}) at 2.25 dS m^{-1} salinity level (Fig 4B). The variable fluorescence (F_v) presented
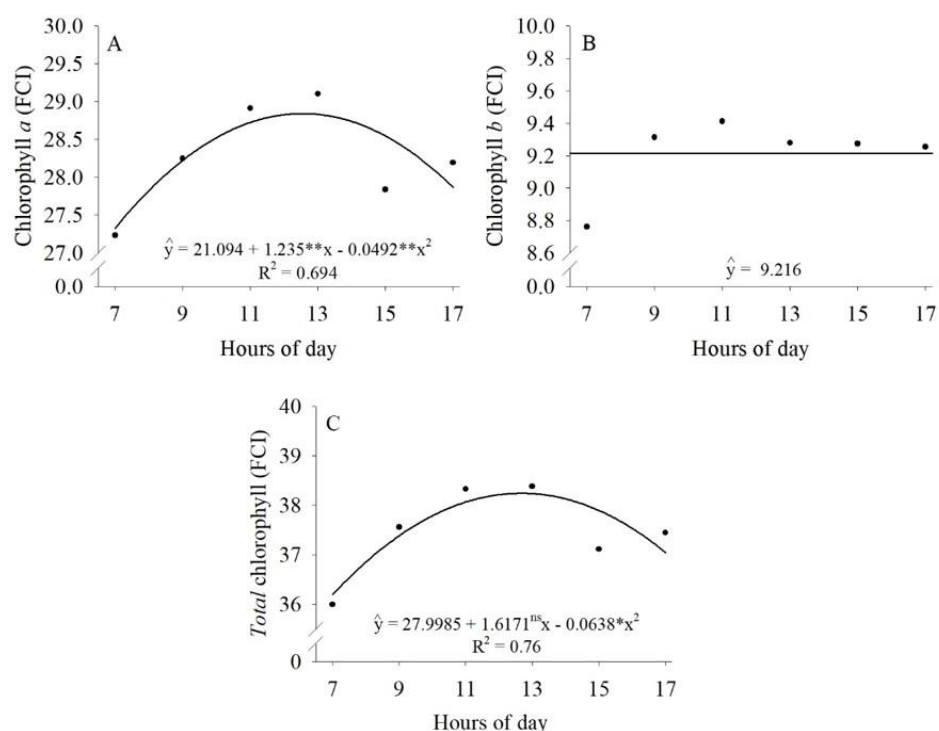
Fig 1. Diurnal variation of chlorophyll *a* (A), *b* (B) and *total* (C) in sugar apple plants (*Annona squamosa*) submitted to salinity stress and nitrogen fertilization. [**, *, ns]: $p<0.01$; $p<0.05$; $p>0.05$, respectively.
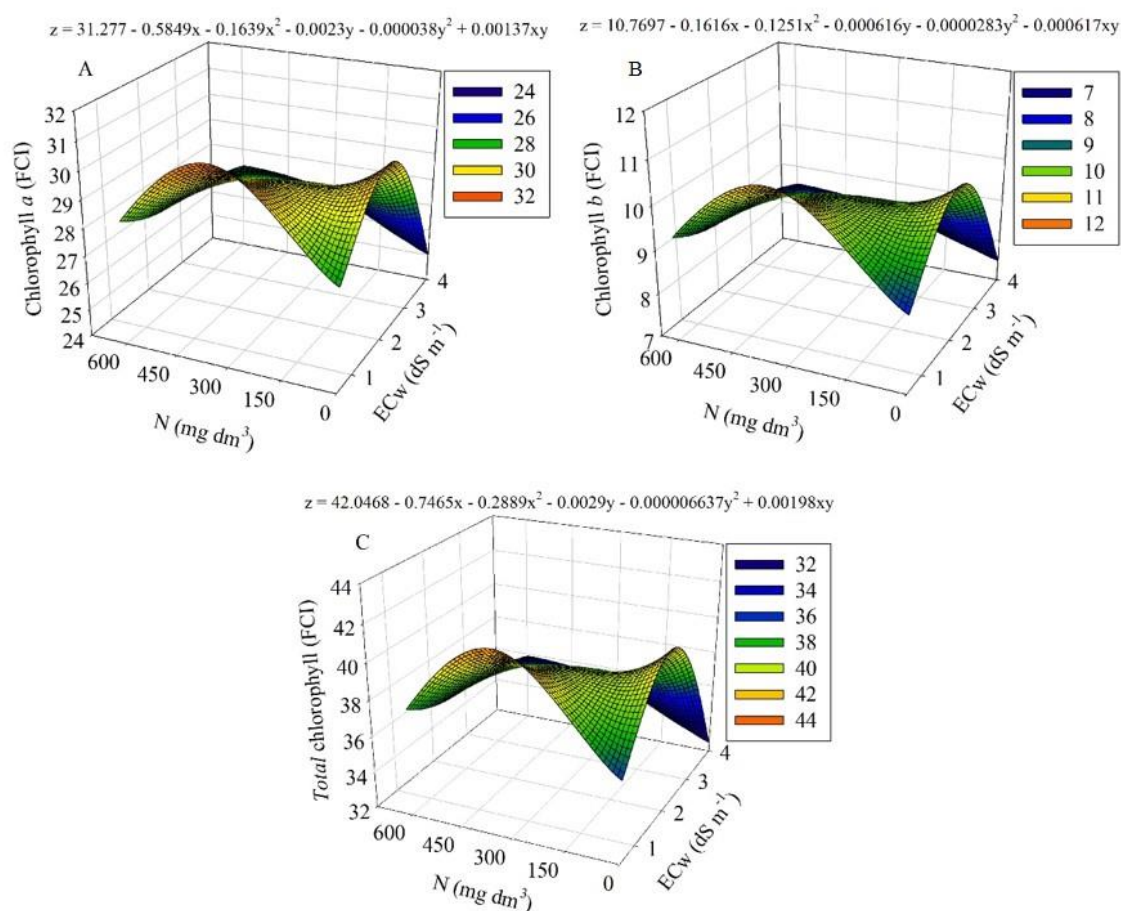

Fig 2. Interaction between the salinity of the irrigation water (EC_w) and nitrogen (N) on chlorophyll *a* (A), *b* (B) and *total* (C) in sugar apple plants (*Annona squamosa*).
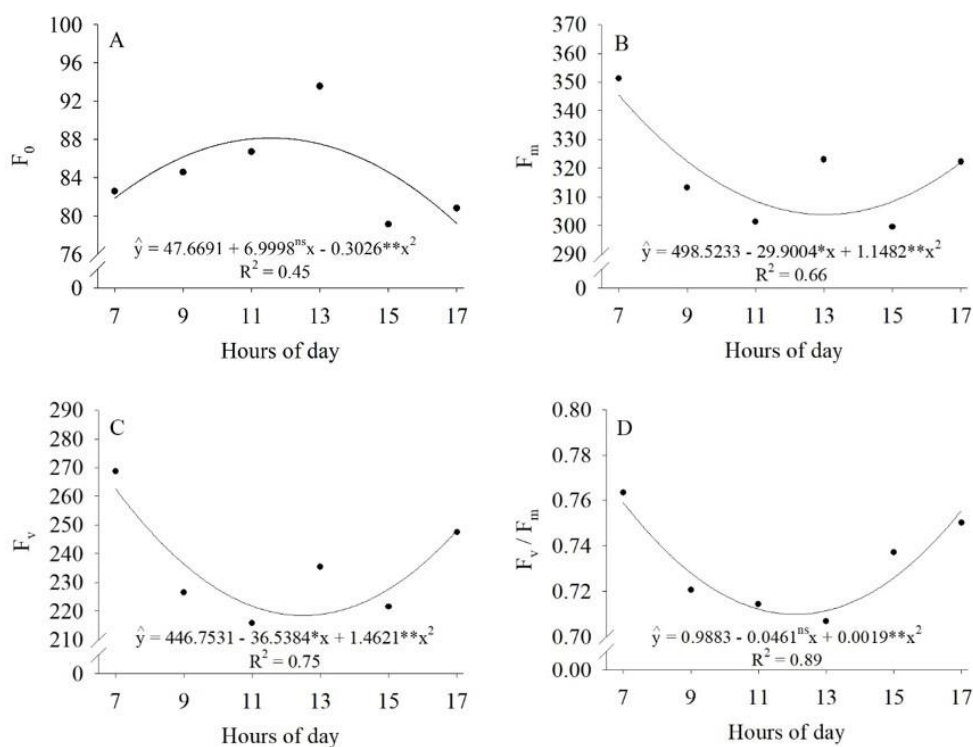
Fig 3. Diurnal variation of initial fluorescence (F_0 - A), maximum fluorescence (F_m - B) variable fluorescence (F_v - C) and photochemical quantum yield of PSII (F_v/F_m - D) in sugar apple plants (*Annona squamosa*) submitted to salinity stress and nitrogen fertilization. *, **, ns: $p < 0.01$, $p < 0.05$, $p > 0.05$, respectively.
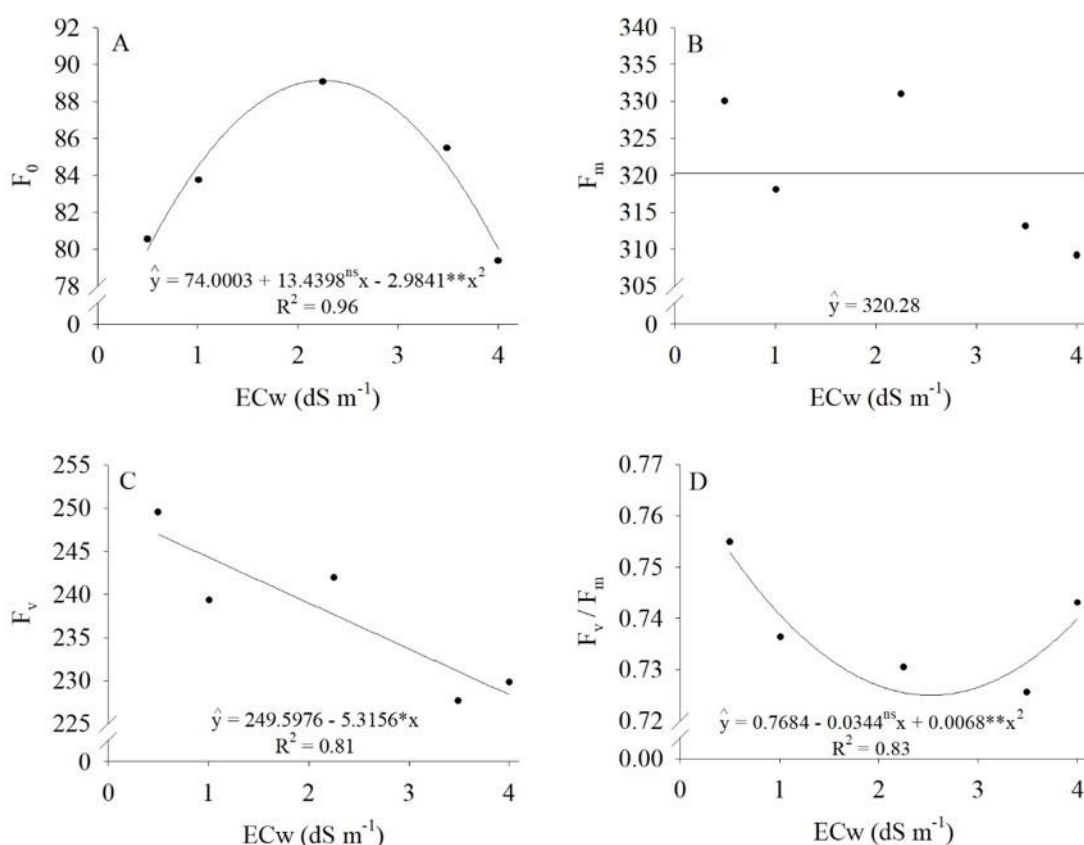

Fig 4. Initial fluorescence (F_0 - A), maximum fluorescence (F_m - B) variable fluorescence (F_v - C) and photochemical quantum yield of PSII (F_v/F_m - D) in sugar apple plants (*Annona squamosa*) submitted to salinity stress. **, *, ns: $p < 0.01$, $p < 0.05$, $p > 0.05$, respectively.
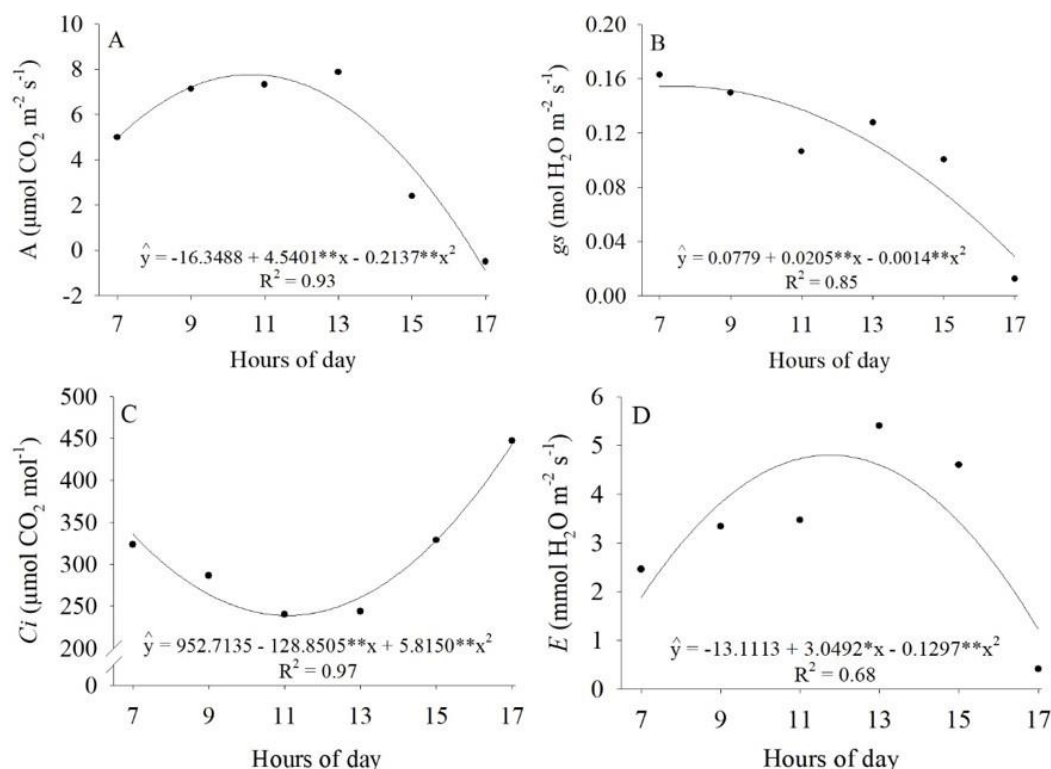
Fig 5. Net CO_2 assimilation rate (A – A), stomatal conductance (gs - B), intercellular CO_2 concentration (Ci - C) and transpiration rate (E - D) as a function of the daily course in sugar apple plants (*Annona squamosa*) submitted to salinity stress and nitrogen fertilization. [**,*]: $p<0.01$, $p<0.05$, respectively.
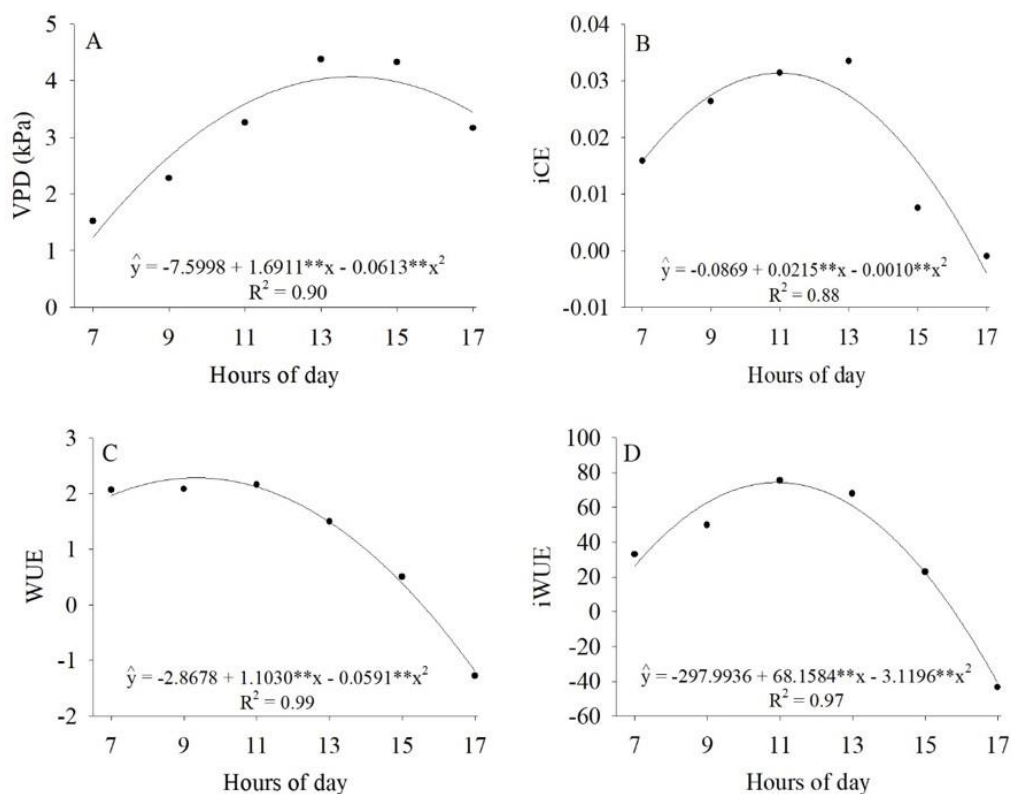

Fig 6. Vapor pressure deficit (VPD - A), instantaneous carboxylation efficiency (iCE - B), water-use efficiency (WUE - C) and intrinsic water-use efficiency (iWUE - D) as a function of the daily course in sugar apple plants (*Annona squamosa*) submitted to salinity stress and nitrogen fertilization.[**]: $p<0.01$.
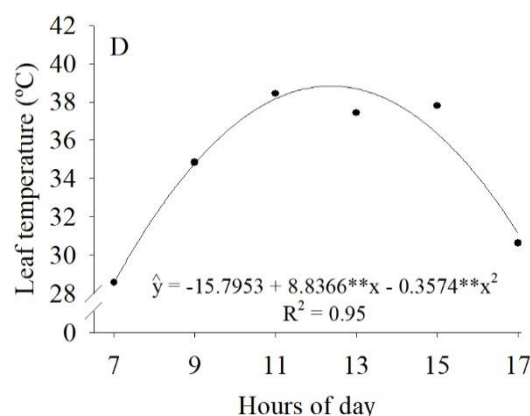
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Fig 7. Leaf temperature (ºC) as a function of the daily course in sugar apple plants (*Annona squamosa*) submitted to salinity stress and nitrogen fertilization. **: $p < 0.01$.

decrease as the salinity level increased (Fig 4C). As for the quantum yield of PSII (F_v/F_m), its values decreased up to the EC_w of 2.25 dS m^{-1}, then it started to increase in the following salinity levels (Fig 4D). This behavior may be due to the plants ability to osmotically adjust to saline environments.

The obtained results are distinct to those found by Marler and Zozor (1996) for the same studied species (*A. squamosa*). According to these authors, the F_v/F_m parameter was not influenced up to the salinity level of 3 dS m^{-1}, however, its values started to decrease as the water salinity level increased. The F_v/F_m values reduction may be due to chlorophyll degradation, especially chlorophyll *a* (Melo et al., 2017). The photosynthetic decline caused by salinity stress generates an excess of energy excitation, which may cause additional damage to the photosystems if not dissipated properly (Mancarella et al., 2016).

Gas exchange

The net CO_2 assimilation rate (*A*), stomatal conductance (*gs*), intercellular CO_2 concentration (*Ci*) and transpiration rate (*E*) values, presented quadratic response to the different assessment times (Figure 5). The net CO_2 assimilation rate highest values were observed at 11:00 a.m. and 1:00 p.m. (7.3 e 7.8 µmol CO_2 m^{-2} s^{-1}, respectively) and gradually decreased through the day (Fig 5A). The net CO_2 assimilation rates reduce throughout the day due to stomatal limitation, which diminish the CO_2 uptake by the leaves (Taiz et al., 2017). This behavior was observed in other species. Santos et al. (2014), studying *Ziziphus joazeiro,* registered the highest net CO_2 assimilation rates during the hottest periods of the day, under optimal light and temperature conditions.

The stomatal conductance highest values were observed in the first assessment time, at 7:00 a.m. (0.16 mol H_2O m^{-2} s^{-1}), and its values decreased in the following assessment times (Fig 5B). This stomatal conductance behavior might have been influenced by the vapor pressure deficit (VPD – Fig 6A), since these parameters have an inversely proportional relationship, where the plant tends to close its stomata to avoid transpirational water loss, especially when submitted to stress conditions (Taiz et al., 2017). Schley et al. (2017) claim that, stomatal conductance became a limiting factor for the net CO_2 assimilation in *Annona emarginata* plants submitted to abiotic stresses.

It can be observed that the intercellular CO_2 concentration decreased in the first hours of the day, due to increased photosynthetic rates. The intercellular CO_2 concentration lowest values were registered at 11:00 a.m. and 1:00 p.m. (240.3, 243.9 µmol CO_2 mol^{-1}, respectively) and the highest at 5:00 p.m. (447.4 µmol CO_2 mol^{-1}) (Fig 5C). Dalastra et al. (2014) state that plants under optimal growing conditions have increased net photosynthesis at high CO_2 concentrations, whilst at low CO_2 concentrations photosynthesis is limited.

The transpiration rates presented similar behavior to the net CO_2 assimilation rates, reaching its peak at 1:00 p.m., with mean value of 5.4 mmol H_2O m^{-2} s^{-1}, and decreasing in the following hours (Fig 5D). Taiz et al. (2017) state that plants transpiration reduces as the solar radiation diminishes throughout the day, due to lower ambient and leaf temperature. Caron et al. (2017) observed similar behavior in *Aleurites fordii* plants, which presented an inversely proportional relationship between its transpiration rates and stomatal resistance, substantiating diminished transpiration rates with stomatal closure.

The vapor pressure deficit (VPD), instantaneous carboxylation efficiency (iCE), water-use efficiency (WUE) and intrinsic water-use efficiency (iWUE), also presented quadratic response to the different assessment times (Fig 6). The VPD increased until 1:00 p.m., reaching the value of 4.3 kPa, and decreasing in the following hours (Fig 6A). The VPD increase might be related to a rise in ambient temperature.

Instantaneous carboxylation efficiency (iCE), presented increasing values until 1:00 p.m., when it reached the maximum peak of 0.033 [(µmol CO_2 m^{-2} s^{-1}) (µmol CO_2 mol^{-1})$^{-1}$] (Fig 6B). This behavior might be explained by observing the net CO_2 assimilation rate pattern, which reached its maximum value at the same time and by the stomatal limitation, that reduces CO_2 diffusion. Scalon et al. (2015) also observed reduced carboxylation efficiency limited by Rubisco, in *Hancornia speciosa* seedlings submitted to water deficit. In the same sense, when studying bean plants under salinity stress and nitrogen fertilization, Furtado et al. (2013) state that the iCE reduction occurred mainly due to decreased photosynthetic rates.

The water-use efficiency showed similar behavior to the stomatal conductance patterns, presenting its highest values during the first periods of the day, reaching its maximum peak at 11:00 a.m. (2.15 µmol CO_2 mol H_2O^{-1}) and decreasing

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in the following hours (Fig 6C). As for the intrinsic water-use efficiency (iWUE) (Fig 6D), the behavior was similar to the net CO_2 assimilation rates (Fig 5A). iWUE values increased until 11:00 a.m., when it reached its maximum peak of 75.39 [(µmol CO_2 m^{-2} s^{-1}) (mmol H_2O m^{-2} s^{-1})$^{-1}$], and gradually decreased in the following hours of the day.

According to Taiz et al. (2017), in C_3 plants, 400 water molecules are required to fix each molecule of CO_2 during photosynthesis, thus the water-use efficiency of those plants is 1/400 or 0.0025. Suassuna et al. (2014) claimed that intrinsic water-use efficiency is maximized when the balance between CO_2 assimilation and transpiration rate is maintained. Leaf temperature behavior is shown in figure 7. The data obtained adjusted to a quadratic behavior as a function of the daily course, with minimum value at 7:00 a.m. and maximum at 11:00 a.m., of 27.5 and 38.06 º C, respectively. The lower temperatures during the first hours of the day supported greater stomatal activity, resulting in increased gas exchanges. The opposite occur under higher temperatures, that is, stomatal closing, resulting in decreased transpiration and CO_2 assimilation rates.

Materials and Methods

Experimental condition and design

The study was carried out at the Center of Agricultural Sciences greenhouse, in the Federal University of Paraíba, located in the city of Areia, state of Paraíba, Brazil. The randomized block experimental design was used, in an incomplete factorial scheme, with five electrical conductivities of the irrigation water (EC$_w$: 0.5, 1.01, 2.25, 3.49 and 4.0 dS m^{-1}) and five nitrogen doses (0, 101, 350, 598.2 and 700 mg dm^{-3}) with four replicates and two plants per plot, derived from the Box Central Composite experimental design matrix. Box Central Composite is an incomplete factorial scheme, where, to generate the number of combinations, the following formula is used: NMT = 2^k + 2.k + 1; NMT = minimum number of treatments; k = number of factors evaluated (Mateus et al., 2001). Urea (45% N) was used as the nitrogen source. The plants fertilized with 700 mg dm^{-3} were drastically damaged and it was not possible to analyze them. The irrigations with the different salinity levels were carried out during the entire conduction of the experiment and the nitrogen doses were applied via single dose at 30 days after sowing (DAS). The different electrical conductivities (EC$_w$) were prepared in non-chlorinated water (0.5 dS m^{-1}) by adding NaCl, CaCl$_2$.2H$_2$O and MgCl$_2$.6H$_2$O in a 7:2:1 ratio. The salts mixture and ratio are equivalent to those found in the Brazilian northeast region waters. For the seedlings formation, 1 dm^3 polyethylene bags filled with horizon A soil collected from the 0-20 cm depth were used. The soil utilized is classified as Planossoil and it had the following chemical characteristics: pH = 6.2; P (Mehlich) = 24.85 mg dm^3; K = 78.42 mg dm^3; Na$^+$ = 0.07 cmol$_c$ dm^3; H$^+$+Al^{+3} = 2.43 cmol$_c$ dm^{-3}; Al^{+3} = 0.00 cmol$_c$ dm^3; Ca^{+2} = 3.90 cmol$_c$ dm^3; Mg^{+2} = 1.90 cmol$_c$ dm^3; SB = 6.07 cmol$_c$ dm^3; CEC = 8.50 cmol$_c$ dm^3; BS = 71.46%; O.M. = 24.83 g kg^{-1}. Three sugar-apple seeds were sown per bag. Following germination, plants were thinned to one plant per bag. No phytosanitary controls were needed during the experiment. Irrigation with saline water started right after the plants were sown, and the plants were irrigated whenever needed to maintain the soil at field capacity. Irrigation management was based on the average of substrate retained water in three drainage lysimeters installed at the treatments location.

Evaluated parameters

At 60 DAS, the physiological parameters were evaluated using the third leaf from the apex of the plant, at six successive 2-hour intervals, from 7:00 a.m. to 5:00 p.m. The gas exchanges were determined with an infrared gas analyzer - IRGA (LI-COR, model LI-6400XT), in one plant of each replicate. The following variables were measured: net CO_2 assimilation rate (A - µmol CO_2 m^{-2} s^{-1}); stomatal conductance (gs - mol H_2O m^{-2} s^{-1}); intercellular CO_2 concentration (Ci - µmol CO_2 mol^{-1}); transpiration rate (E - mmol H_2O m^{-2} s^{-1}); vapor pressure deficit (VPD$_{leaf-air}$ - kPa) and leaf temperature (°C). Subsequently to the data collection, water-use efficiency (WUE - A/E), intrinsic water-use efficiency (iWUE - A/gs) and instantaneous carboxylation efficiency (iCE - A/Ci) were calculated.

Chlorophyll fluorescence emission was determined according to the method described by Melo et al. (2017), using a modulated fluorometer (Plant Efficiency Analyser PEA II® - Hansatech Instruments Co., UK). The following fluorescence parameters were determined: initial fluorescence (F$_0$), maximum fluorescence (F$_m$), variable fluorescence (F$_v$ = F$_m$ - F$_0$) and quantum yield of photosystem II (F$_v$/F$_m$). Chlorophyll a, chlorophyll b and *total* chlorophyll levels were determined by a non-destructive method using the portable chlorophyll meter ClorfiLOG® (model CFL 1030) and expressed as the Falker Chlorophyll Index (FCI).

Data analysis

The data were submitted to ANOVA *F*-test at the level of 5% probability. Polynomial regression analyses were performed in the cases of significance, using the statistical program SAS University (Cody, 2015).

Conclusion

There are ecophysiological variations throughout the day in sugar apple plants (*Annona squamosa*) submitted to salinity stress and nitrogen fertilization. There is significant interaction between the electrical conductivity of the irrigation water and nitrogen fertilization for the chlorophyll indexes. The electrical conductivity of the irrigation water caused significant effects on chlorophyll fluorescence. Therefore, it can be stated that the sugar apple plants ecophysiology varies throughout the day and the salinity of the irrigation water affects its chlorophyll content and fluorescence.

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