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Review

Mechanisms of aerenchyma formation in maize roots

Imene Rajhi* and Haythem Mhadhbi

Laboratory of Legumes, Biotechnology Center, Borj Cedria Science and Technology Park, Route Touristique Borj Cedria-Soliman, B.P. 901, 2050 Hammam-Lif, Tunisia.

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Respiration is very sensitive to waterlogged conditions. Under these conditions, plant roots suffer from lack of available oxygen. In fact, waterlogging reduces the exchange of gases between the plant and the atmosphere. When plants cannot receive sufficient oxygen level for respiration, they form aerenchyma in their roots which function as reservoirs of oxygen in the submerged plant. Aerenchyma is formed in maize (*Zea mays*) roots in response to different types of stress such as waterlogging, mechanical impedance, drought and nutrient deficiencies. Ethylene plays a crucial role in aerenchyma formation. Under waterlogged conditions, it can be cumulated in the submerged tissue and induces genes implicated in aerenchyma formation. These genes are related to calcium signaling, cell wall degradation and reactive oxygen species (ROS). In this review, the authors focused on the recent findings on aerenchyma in maize roots and explained the mechanisms of its formation under waterlogged conditions.

Key words: Aerenchyma, maize root cortex, waterlogging, ethylene, programmed cell death.

INTRODUCTION

Respiration is one of the plant physiological processes, which is defined as the exchange of gases between air and cells within tissues. Oxygen and carbon dioxide are considered as the most important gases for respiration which are diffused in an opposite direction into and out the plant. Under natural conditions, oxygen and carbon dioxide are transported into or out of the plant's root via soil pores filled with air. Respiration is very sensitive to waterlogged conditions because the excess of water reduces the exchange of gases between the plant and the atmosphere. When the soil pores are filled with air, oxygen can easily diffuse into the plant's root but this diffusion is decreased when the soil pores are filled with water. Indeed, the diffusion of gases through air is 10^4 fold faster than in water (Colmer and Voesenek, 2009). Additionally to the scarcity of oxygen in submerged conditions, the available oxygen will be also consumed by the microorganisms' resident in the soil. As a result, oxygen level decreases in underwater tissues. However, the carbon dioxide level increases due to the microbial and root respirations (Colmer and Voesenek, 2009). This deficiency of oxygen alters nutrient and water uptake in water-stressed plants causing the diminution of the total root volume (Bailey-Serres and Voesenek, 2008). Most of the higher plants are very sensitive to waterlogged conditions and their growth and yields can be negatively

*Corresponding author. E-mail: imenrajhi@yahoo.fr.

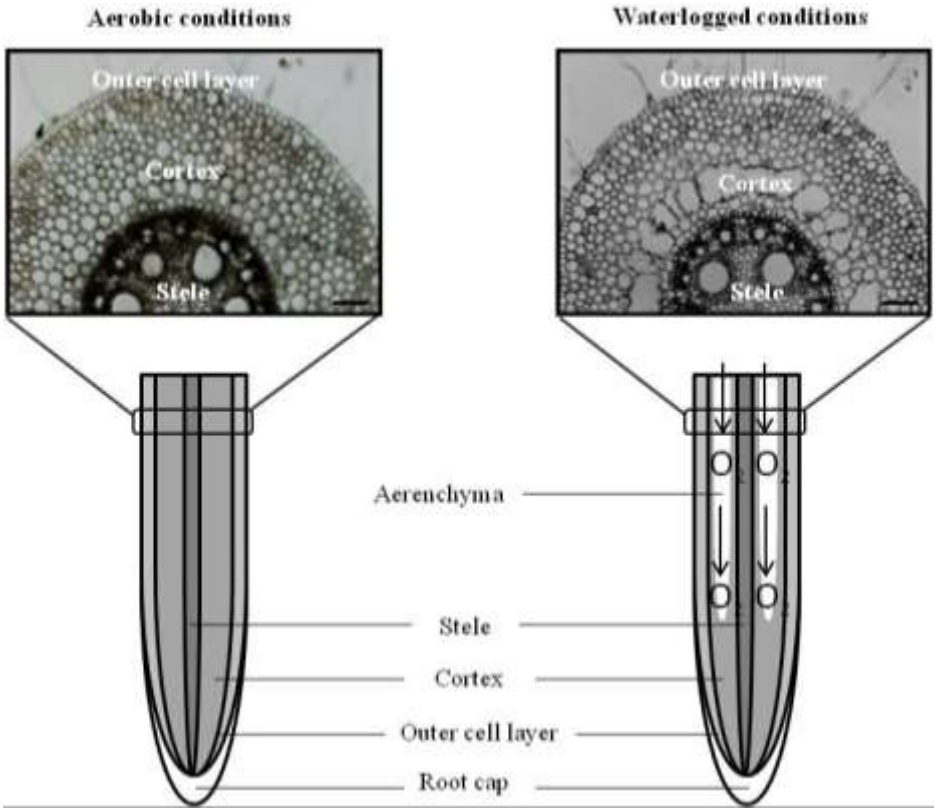

Figure 1. *Zea mays* roots grown under two different conditions; aerobic and waterlogged conditions. The cross-sections show the inducible lysigenous aerenchyma in maize roots under waterlogged conditions. Scale bar: 0.1 mm (Rajhi et al., 2011).

impacted. Plants cannot survive for long periods under these conditions because oxygen quantity is depleted in flooded soil within 48 h (Purvis and Williamson 1972; Fausey and McDonald, 1985). Plant tolerance to low oxygen availability differs between the species. In fact, only few plants can grow in waterlogged soils, such as rice which is known to be highly tolerant to flooding (Mustroph and Albercht, 2003). To escape the oxygen shortage problem, several transformations at the anatomical, morphological and metabolic levels take place in immersed tissues. The formation of aerenchyma is considered as the main important adaptation to the waterlogged conditions. It can be formed in shoots and roots of a large number of plant species such as maize (He et al., 1996a). Many reviews are emphasized on the morphological, anatomical, pharmacological and molecular studies of aerenchyma formation. In this review, the recent discoveries related to aerenchyma formation in maize roots under waterlogged stress is summarized.

TYPES OF AERENCHYMA

Aerenchyma is a tissue composing of longitudinal gas spaces separated by the strands of living cells, found in the root cortex of waterlogged plants as shown in Figure 1. Aerenchyma is formed by one of the two well described mechanisms: schizogeny or lysigeny. Schizogenous aerenchyma is formed by creating gas spaces between cells as a result of highly-regulated cell separation and differential cell expansion, without the death of the cells (Laan et al., 1989). Lysigenous aerenchyma is formed by creating gas spaces as a result of programmed cell death (PCD) in the cortical region of the root (Gunawardena et al., 2001a). Lysigenous aerenchyma is observed in many crops such as flooding tolerant rice, moderately tolerant wheat and intolerant maize (Mustroph and Albercht, 2003). Aerenchyma can be formed by both mechanisms in some species such as *Saggitaria lancifolia* (Schussler and Longstreth, 1996). In maize roots, lysigenous aerenchyma is formed by the death of cells in the mid cortex in a zone behind the apical root. Lysegineous aerenchyma is developed by the digestion of the longitudinal and radial cells separated by live cells attaching the stele and epidermis (Gunawardena et al., 2001a). The walls and the contents of the digested cells completely disappeared (Gunawardena et al., 2001a; Drew et al., 1980). Aerenchyma can be induced in response to stress or constitutively formed. Lysigenous

aerenchyma in many of the wetland plants is developped constitutively in their roots under normal growth conditions such as rice and *Juncus effusus* and its formation is intensified when the soil is saturated with water. In the dryland (non-wetland) plants, such as maize, lysigenous aerenchyma is induced by waterlogging conditions (Drew et al., 1979), mechanical impedance, hypoxia (He et al., 1996b), drought (Zhu et al., 2010) and by nutrient deficiency (He et al., 1992; Vassilis et al., 2012; Postma and Lynch, 2011).

INDUCTION OF AERENCHYMA BY EXTERNAL STIMULI

Induction by waterlogging

Gas spaces aerenchyma in the root cortex is formed in response to hypoxia. One of the important functions of aerenchyma is to enhance oxygen transport, where the shortage of oxygen may prevent submerged root respiration (Drew et al., 1979).

Induction by drought

In order to diminish root metabolic rate to provide greater plant growth and water aquisition, maize roots develop aerecnhyma in response to drought stress. Under drought conditions, the biomass production and yield of maize genotypes, which develop more aerenchyma, had respectively five and eight times greater than genotypes which develop less aerenchyma (Zhu et al., 2010).

Induction by nutrient deficiencies

Maize roots develop aerenchyma when the soil suffers from the deficiency of the nitrate, phosphate or sulphate (Konings and Verschuren 2003; Bouranis et al., 2003; Vassilis et al., 2012). The mechanisms involved in the formation of aerenchyma under these conditions are still unclear. Under nutrient deprivation (nitrate, phosphate and sulphate), signs of PCD were observed at 1 cm behind the root tip of six-day old maize seedlings. The PCD caused by the nutrient deficiency is called nPCD (Vassilis et al., 2012). It has been demonstrated that ROS production may also contribute to aerenchyma formation due to nutrient deficiency (Bouranis et al., 2003). Vassilis et al. (2012) demonstrated that ROS and calcium are involved in the initiation of PCD. In addition, the objective of the development of aerenchyma in response to phosphorous deprivation is the reduction of the respiration and phosphorous content in the root tissue (Postma and Lynch, 2011). Deficiencies of nitrate, phosphate or sulphate increase the sensitivity of cortical cells to ethylene which promotes more cells lysis (Drew et al., 1979; Bouranis et al., 2003). Ethylene can be considered as a general stress hormone arbitrated responses to hypoxia, drought and a number of nutrient deficiencies and it plays a crucial role in aerenchyma formation in maize roots under different stress conditions (He et al., 1992; Schachtman and Goodger, 2008; Borch et al., 1999; Brown et al., 2003; Postma and Lynch, 2010).

AERENCHYMA FUNCTION

When plants cannot receive sufficient oxygen quantity for respiration, they develop aerenchyma in their roots. Aerenchyma is very important for the survival of the plants under waterlogged conditions. It minimizes the consumption of total oxygen per unit surface of the root by the formation of air cavities in place of living cells. It is the principal oxygen reservoir and the best ventilation system in the immersed tissue. Aerenchyma allows the passage of gases in and out of tissues in plant roots, petioles and stems. Oxygen is provided to the roots by aerenchyma, while other gases (carbon dioxide, ethylene and methane) are transported from the soil and the root to the shoot and the atmosphere (Armstrong, 1979). The oxygen can be transported by simple diffusion or a consequence of pressure flow. It can be offered from photosynthesis or from the atmosphere. Aerenchyma plays an important role in protecting the root tip from the harmful effect of anoxic soils (such as phytotoxins and organic compounds, Fe^{2+} and Mn^{2+}) by increasing the oxygen concentration of the rhizosphere (Mergemann and Sauter, 2000).

MECHANISMS OF AERENCHYMA FORMATION

Implication of ethylene in aerenchyma formation

Ethylene, the plant gaseous hormone, which is a simple hydrocarbon that can diffuse into and out of plant tissues from both endogenous and exogenous sources, plays a central role in hypoxic stress signaling (Watkins, 2006). Ethylene is produced from methionine that is first converted to S-adenosylmethionine (AdoMet) by S-adenosylmethionine synthase. AdoMet is then converted to 1-aminocyclopropane-1-carboxylate (ACC) by ACC synthase (ACS). ACC oxidase (ACO) generates ethylene by oxidizing ACC in a reaction that also produces carbon dioxide (CO_2) and hydrogen cyanide (HCN). The plant hormone ethylene is implicated in regulating cell death processes (Jackson et al., 1985). Actually, many of the adaptive growth responses take place in response to ethylene which is cumulated in underwater tissues (Drew et al., 1981). This accumulation is due to the reduced diffusion from the plant to the surrounding water and the induction of the biosynthesis of this hormone by stress

conditions (Drew et al., 1981). This hormone plays a central role in aerenchyma formation in maize roots. Under hypoxic conditions, maize roots act in response by inducing the expression of the ethylene biosynthetic machinery leading to the increase in ethylene production (Geisler-Lee et al., 2010). The process of PCD, which appears to occur in the roots of maize during the formation of lysigenous aerenchyma, appears to be regulated by ethylene (Rajhi et al., 2011; Yamauchi et al., 2011; Takahashi et al., 2015). The hypoxic treatment increased ethylene production in maize roots several fold within 3 h when compared with aerobic conditions. A 5.8 fold was observed at six hours after treatment and the maximum of ethylene evolution (10 fold) was detected at 12 h after the treatment (Geisler-Lee et al., 2010). Treatment of maize roots with inhibitors of ethylene action (e.g., silver ions) or ethylene biosynthesis [e.g., aminoethoxyvinylglycine (AVG), aminooxyacetic acid (AOA) and cobalt chloride] effectively blocks aerenchyma formation under hypoxic conditions (Drew et al., 1981; Konings, 1982). The use of 1-methylcyclopropene (1-MCP), an inhibitor of ethylene perception, totally blocks aerenchyma formation in maize roots under hypoxic conditions (Rajhi et al., 2011). Moreover, aerenchyma can be induced by treatment with ethylene even under aerobic conditions (Jackson et al., 1985; Takahashi et al., 2015). In wheat, Lysigenous aerenchyma formation was induced by ACC treatment (Yamauchi et al., 2014). These observations indicate that ethylene works as a trigger for inducible lysegenious aerenchyma in maize roots.

Aerenchyma formation via cell death

Cell death signs

The first signs of cell death during aerenchyma formation were detected in maize cells. The nuclear DNA fragmentation is considered to be a distinctive characteristic of animal cells apoptosis. Analyze of *in situ* terminal deoxynucleotidyl transferase-mediated dUTP nick-end labelling (TUNEL) applied to maize roots treated by ethylene or hypoxia suggested internucleosomal cleavage of DNA (Gunawardena et al., 2001a). Cytoplasmic changes including plasma membrane invagination and the formation of vesicles was detected before chromatin condensation (Gunawardena et al., 2001a), which is considered to be the first event in animal apoptosis. The major distinctive event in animal cells apoptosis is the formation of apoptotic bodies. This event was also confirmed by Gunawardena et al. in (2001a). In fact, a cellular condensation, condensation of chromatin and the presence of intact organelles surrounded by membrane similar to apoptotic bodies were detected in maize roots treated by ethylene or hypoxia. Aerenchyma formation in maize roots induced by ethylene or hypoxia shows characteristics in part, similar to both apoptosis and cytoplasmic cell death in animal cells. Aerenchyma formation in maize roots appears to be a form of programmed cell death (Campbell and Drew, 1983).

Cell wall degradation

In the final stage of the formation of the lysigenous aerenchyma, the cell wall is enzymatically degraded. In the begining, the localizations of esterified pectin and de-esterified pectin in cell wall of the maize cortex tissue are modified during cell death, then the cell wall is degraded by the combined actions of pectolytic, xylanolytic and cellulosolytic enzymes (Gunawardena et al., 2001a). Indeed, the activities which are involved in loosening or degrading the cell wall including cellulase, xylanase and pectinase, are increased in maize roots under waterlogged conditions. Several genes related to cell wall loosening and degradation such genes encoding xyloglucan endotransglucosylase, polygalacturonase and cellulase were up-regulated specifically in the cortical root cells under waterlogged conditions and their expression is repressed by the treatment of 1-MCP, an inhibitor of ethylene perception, under the same conditions (Rajhi et al., 2011). Both, the treatment of maize roots under hypoxic conditions or with a high ethylene concentrations, can induce remarkable augmentation in cellulase activity within 3 days (He et al., 1994) as well as increases in pectinase and xylanase activities (Bragina et al., 2003). Besides, it has been established that a xyloglucan endotransglycolase homolog in maize, which is induced by both ethylene and flooding, is related to aerenchyma formation (Sachs et al., 1996). In fact, treatment with an ethylene biosynthesis inhibitor, aminooxyacetic acid (AOA), under flooded conditions avoided the spread of aerenchyma in maize roots and totally restrained the accumulation of XET mRNA.

Involvement of reactive oxygen species in aerenchyma formation

Recently many reports show that reactive oxygen species (ROS) play an important role in plant cell death, defense and growth (Steffens and Sauter, 2009; Yoshioka et al., 2009; Steffens and Sauter 2011). ROS include molecules (hydrogen peroxide and ozone), ions (hypochlorites) and radicals (hydroxyl and superoxide). The major source of ROS in plants is the NADPH oxidase (NOX) that catalyze conversion of dioxygen (O_2) to the superoxide radical (O_2^-) which ultimately leads to the production of hydrogen peroxide (H_2O_2). In plants, the NOX homologs have been named respiratory burst oxidase homologs (Rboh) and they are also involved in ROS production in response to pathogens, plant defense, development, hormone biosynthesis and cellular signal transduction (Sagi and Fluhr, 2001; Torres et al., 2002; Foreman et al., 2003). It has been demonstrated that the hydrogen peroxide operates as a signal for ethylene-induced epidermal cell

death (Steffens and Sauter, 2009, 2005). Additionnaly, the hydrogen peroxide stimulates aerenchyma in the rice stem (Steffens and Sauter, 2010). In rice, the NADPH oxidase controls the H_2O_2 which regulates epidermal cell death before the emergence of adventitious roots (Steffens and Sauter, 2009, 2005). The inhibitor of NADPH activity diphenylene iodonium (DPI) decreased the rates of cell death in rice epidermal cells (Steffens and Sauter, 2009). In fact, the use of an ethylene-releasing compound, ethephon, enhances ROS generation and increases aerenchyma in rice. Under carbon starvation, the DPI inhibited the O_2^- production from NADPH oxidase (Rboh) and cell death in carrot (*Daucus carota*) cells (Chae and Lee, 2001). In wheat, the treatment of the roots with ACC and DPI partly suppressed the aerenchyma ACC-induced responses (Yamauchi et al., 2014). In addition, the pre-treatment of wheat seedlings with ACC increased the expression of three genes encoding respiratory burst oxidase homologue. Among three *TaRboh* genes the expression level of the *TaRboh* gene was highest in the first seminal roots immediately after pre-treatment with ACC. However, *TaRboh* expression was highest at 72 h after initiation of growth under stagnant conditions (Yamauchi et al., 2014). In maize seedlings, treatment with 1-MCP repressed the expression of Rboh gene in the root cortical cells under waterlogged conditions. The expression of Rboh gene under hypoxic conditions is highest in cortical cells than in stellar or outer layer cells. Treatment of maize seedlings with DPI under waterlogged conditions reduced aerenchyma formation. This indicates that Rboh in maize is involved in aerenchyma formation specifically in the cortex of the root (Rajhi et al., 2011).

On the other hand, the expression of the gene encoding metallothionein, which works as a ROS scavenger (Wong et al., 2004), was repressed under waterlogged conditions in the cortex of maize roots and that the repression seemed to be ethylene dependent. The cortical cell-specific down-regulation of the maize metallothionein gene may contribute to higher accumulation of the RBOH-produced H_2O_2, which induces cell death in the cortical cells for lysigenous aerenchyma formation (Rajhi et al., 2011). Interestingly, the rice Metallothionein2b (MT2b) gene is down-regulated in response to ethylene and H_2O_2 in epidermal cells, thereby amplifying the accumulation of H_2O_2 produced by NADPH oxidase, to induce cell death (Steffens and Sauter, 2009, 2010). These observations raise the possibility that, waterlogging-induced up-regulation of Rboh is involved in H_2O_2 production and the H_2O_2 induces aerenchyma cell death in root cortical cells, which is cotrolled by ethylene.

Implication of calcium signaling

Calcium-dependent signaling pathways are involved in the process of lysigenous aerenchyma formation in maize roots (He et al., 1996b). Many studies have suggested that the cytosolic calcium ion (Ca^{2+}) functions as a second messenger for signaling pathways in response to oxygen deprivation (Subbaiah et al., 1994; Tsuji et al., 2000; Baxter-Burrell et al., 2002). Ca^{2+} signaling may also be involved in aerenchyma formation in maize roots (He et al., 1996b). Several genes implicated in calcium signaling, whose expressions were significantly induced specifically in the maize root cortex under the waterlogged conditions were identified such as genes encoding EF hand family protein (Calcineurin B like), calmodulin like protein, C2 domain containing protein and EH domain containing protein. The calcium-dependent protein kinase activates Rboh by phosphorylation of its N-terminal region (Kobayashi et al., 2007). It has been reported that an interaction between the Ca^{2+} signaling and the RBOH-mediated H_2O_2 production might be important for the programmed cell death in the root cortical cells (Rajhi et al., 2011).

CONCLUSION

In conclusion, this study aimed to (i) clarify the meaning of aerenhyma formation and its role under different stresses especially under waterlogging conditions and (ii) try to understand the mechanism of formation of air spaces in the root cortical cells.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interest.

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Yield of the hydroponic lettuce under levels of salinity of the nutrient solution

P. F. Silva[1*], R. M. Matos[2], S. M. Bonou[2], T. G. Sobrinho[2], V. E. Borges[2], J. Dantas Neto[2] and A. P. Melo Júnior[3]

[1]Postgraduate Program in Natural Resources, Center for Technology and Natural Resources, Federal University of Campina Grande, Campina Grande – Paraíba, Brazil.
[2]Academic Unit of Agricultural Engineering, Center for Technology and Natural Resources, Federal University of Campina Grande, Campina Grande – Paraíba, Brazil.
[3]Instituo Federal do Sertão Pernambucano – Pernambuco, Petrolina, Brazil.

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Hydroponic cultivation is a viable alternative, given the water scarcity scenario, since this technique uses water rationally and without waste. However, it is necessary to monitor the salinity of the nutrient solution, especially in leafy vegetables such as lettuce. The aim of this research is to examine the yield of hydroponic lettuce under different salinity levels of the nutrient solution, in greenhouse. The experiment was conducted in a hydroponic system installed in a greenhouse belonging to the Federal University of Campina Grande. The experiment was carried out in a randomized block design, in a 5 x 2 factorial scheme: the first factor is five salinity levels of the nutrient solution (S1 = 1.0, S2 = 1.3, S3 = 1.6; S4 = 1.9 and S5 = 2.2 dS m^{-1}) and the second factor is two lettuce cultivars (Robusta and Bs55), with three replicates. The isolated cultivar factor did not significantly influence any of the analyzed variables of the hydroponic lettuce. The different levels of salinity of the nutrient solution positively influenced the variables analyzed: leaf area, SPAD index, chlorophyll a, b and total, and yield of leaves of hydroponic lettuce. Hydroponic lettuce can be grown up to 2.2 dS m^{-1} of electrical conductivity of the nutrient solution without any loss in yield.

Key words: *Lactuca sativa* L., hydroponic, chlorophyll, electrical conductivity.

INTRODUCTION

Lettuce (*Lactuca sativa* L.) is one of the leafy vegetables mostly present in the diet of Brazilian population. It is a source of vitamins and minerals in the diet of the population and is notable for its low caloric value; it is widely used in balanced diets and recommended by nutritionists. It occupies an important part of the national market and acquires an increasing importance in the country's economy (Filgueira, 2008; Lima et al., 2008; Lopes et al., 2011).

According to Aquino et al. (2007), because it is a sensitive crop to adverse climatic conditions, an alternative to minimize this situation is the cultivation in protected environment of the vegetable. In this context, hydroponic cultivation represents an advantageous

*Corresponding author. Email: patrycyafs@yahoo.com.br.

alternative when compared to conventional cultivation, to obtain superior products, more uniform, with higher yield, lower labor costs, lower consumption of water and agricultural inputs, besides the environment preservation (Paulus et al., 2010).

In the semi-arid region of Brazil, most of the producers use water collected in surface reservoirs for the cultivation of vegetables, which can present high concentrations of salts, where values of relatively high electrical conductivity are often found (Costa et al., 2004; Souza Neta et al., 2013).According to Soares et al. (2007). A viable alternative may be the use of saline waters in hydroponic crops, since the tolerance of plants to salinity in this cultivation system is greater than the conventional system. Among the hydroponic producers, lettuce is the most widespread crop due to its short cycle and guarantee of economic return, and the most commonly used technique is the Laminar Nutrient Film (NFT = Nutrient Film Technique) (Alves et al., 2011; Paulus et al., 2012). However, specialized technical follow-up is necessary in order to have the balanced nutrient solution, that provides adequate nutrition to the plants and to avoid the effect of the toxicity of some ions to the plants.

Currently, research has been developed to provide information for the use of waters with relatively high levels of salts as an input for the leafy vegetables cultivation hydroponic system (Santos et al., 2010; Paulus et al., 2010; Alves et al., 2011; Souza Neta et al., 2013).However, there are still few studies developed for the lettuce culture submitted to saline stress, where in the already developed studies different effects were observed, thus demonstrating that more studies need to be developed.

In view of the above, the aim of this research is to examine the yield of the hydroponic lettuce under different salinity levels of the nutrient solution, in greenhouse.

MATERIALS AND METHODS

Characteristics of the experimental area

The experiment was carried out in a greenhouse belonging to the Federal University of Campina Grande (UFCG), located in the municipality of Campina Grande, Paraíba State, Brazil, under the geographical coordinates of 7° 13' 11" South latitude, 35° 53' 31" of West longitude and altitude of 550 m. The greenhouse is of the chapel type and has a structure in galvanized arches, with dimensions of 6.0 m width, 10 m in length and 3.00 m ceilings; it is covered with glass fiber tiles, and sides wrapped with screen that allow the partial passage of the wind, softening the internal temperature. The structure has five alternative hydroponic system benches with PN40 PVC pipes, spaced from each other by 0.60 m, with initial height of 0.76 m and slope of 2%. The profiles are spaced at 0.20 m and have a length of 3.0 m as a simplified layout (Figure 1). The seedlings were produced in phenolic foam substrate for germination and rooting. These foams were previously washed with running water, to eliminate possible remaining residues of their manufacture. The development of the seedlings was done in a hydroponic structure, called nursery. Transplanting was performed when lettuce seedlings presented four definitive leaves, seven lettuces were seedlings spaced at 0.20 m between plants, in each laminar flow profile of nutrients. During the experimental period, data were collected on the temperature and relative humidity of the air, from transplanting to harvesting, corresponding to 21 days after transplanting (DAT). Data were collected through a Digital Hygrometer installed inside the greenhouse.

Design, treatments and planting system

The experiment was organized as a randomized block design (RBD), arranged in a 5 x 2 factorial scheme. The first factor consisted of five salinity levels of the nutrient solution (S1 = 1.0, S2 = 1.3, S3 = 1.6; S4 = 1.9 and S5 = 2.2 dS m^{-1}) and the second factor, two cultivars of curly lettuce: Robusta and Bs55. Three replicates were used, corresponding to 10 treatments and 30 experimental units; each unit experimental plant was composed of 6 plants. It is necessary to mention that two plants were left as a border: the first and the last plant in each laminar flow profile of nutrients, with a total of 210 plants. The profiles were labeled with each treatment and their respective replication.

System characteristics and nutrient solution management

The profiles for each treatment were interconnected to rigid plastic reservoirs with a capacity of 100 liters (a total of 5 reservoirs), where the nutrient solutions were stored, corresponding to each treatment. Each reservoir consisted of an EMICOL Class H 322139 electro-pump, with a flow rate of 900 L h^{-1}. Each electric pump was connected to an analog timer, connected to the electric power, to keep the solution circulating automatically. The timers were programmed to start or stop the pump every 15 min.

The preparation and management of the nutrient solution was according to the recommendation of Furlani et al. (1999) for all treatments. The formulation used to prepare the solution was composed of HidrogoodFert, which contains all the macronutrients and micronutrients necessary for the proper development of the culture. The compound was added to the water along with Calcium Nitrate and Iron Chelate. For the treatments S1, S2, S3, S4 and S5 the solution was prepared with rainwater, due to the low salinity that presents 0.245 dS m^{-1}. The daily monitoring of the solutions to guarantee the electrical conductivity in each treatment was carried out. The Mca 150 benchtop conductivity meter was used twice a day. When necessary, it was adjusted by dilution of the treatment with a nutrient solution. It was previously prepared with rainwater and stored in an extra reservoir, as recommended by Furlani et al. (1999), or by addition of NaCl, if necessary to concentrate the solution further. The hydrogen potential (pH) was quantified daily through a bench pHmeter model LUCA-210, to be maintained between 5.5 and 6.5 (due to the optimal range for nutrient uptake by the crop); it can be adjusted when necessary, through a base solution composed of sodium hydroxide or an acid solution composed of sulfuric acid.

Variables analyzed

The evaluation was performed at 21 days after transplanting of the seedlings, where the following variables were analyzed: leaf area with LI 3100 portable meter; relative chlorophyll content (SPAD index); content of chlorophyll a, b, and total; carotenoids content and the yield of lettuce leaves. The relative chlorophyll content (SPAD index) was determined on the fourth fully expanded leaf, from the apex. Measurements were performed between 7 and 9

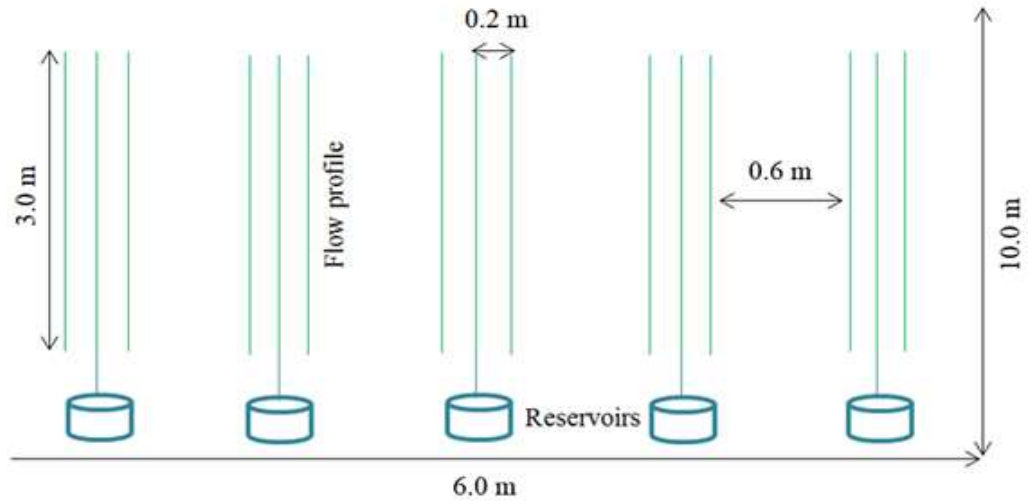

Figure 1. Layout of the hydroponic cultivation system.

o'clock in the morning, using the portable chlorophyll meter SPAD-502. Three measurements of the SPAD index per leaf were performed in the central region of the leaf limb of each plant of the useful plot, in each treatment, and the mean was used to represent the treatments. For determination of chloroplastidic pigments (chlorophyll "a", "b", total and carotenoids), the leaves were collected and immediately packed in aluminum envelopes, stored in thermal insulated containers containing chemical ice and transported immediately to the laboratory. Then, with the aid of a circular nozzle, circles of vegetable tissue were removed from the middle third of the leaves, and each material was weighed.

Subsequently, the material was macerated and placed in aluminum-coated containers, adding 6.0 ml of 80% acetone. The containers were refrigerated at 8.0 ° C for 24 h and thereafter were paper filtered for 5 min according to methodology proposed by Arnon (1945). Absorbance readings were obtained by spectrophotometry at wavelengths of 470 (A470), 647 (A647) and 663 nm (A663), using 80% acetone as white In the quantification of chlorophyll "a", "b", total and carotenoids. The equations described by Lichtenthaler (1987) were used. The yield of the lettuce leaves was determined based on the total fresh and commercial weight. That is, those leaves superior to 10.0 cm in length and that did not present any physical defect were weighed in a precision scale, where this procedure was realized in treatment.

Statistical analysis

The variables were analyzed statistically by F test, unfolding the analysis whenever the interaction was significant. The quantitative factor of the salinity levels was statistically analyzed by means of polynomial regression (linear and quadratic). The cultivars were analyzed using the Tukey test at 5%, with the computer program Sisvar, according to Ferreira (2011).

RESULTS AND DISCUSSION

Temperature and air relative humidity

The data of temperature and relative humidity of the air observed within the greenhouse from transplanting to harvest of the lettuce are shown in Figure 2. The mean air temperature during the experimental period was 26.7°C, the mean maximum temperature was 30.3°C and the mean minimum was 23.1°C. While the mean air humidity during the 21 days of cultivation was 68.4%, the average maximum was 77.3% and the mean minimum was 59.6% (Figure 2A and B). The climatic conditions assured inside the greenhouse were favorable for the development of lettuce. These temperatures are favorable to the growth and development of lettuce (Paulus et al., 2010; Silva et al., 2018).

Salinity levels

In the conditions under which the experiment was developed, when using rainwater in the preparation of the nutrient solution, it was verified that there was a slight reduction of the salinity of the nutrient solution due to the nutrient consumption. In this case it was superior to the accumulation of dissolved nutrients in the nutrient solution (Table 1). Corroborating with Paulus et al. (2010) who verified a similar effect for the treatment with non-saline water, they found that nutrient consumption is higher than the accumulation of salts dissolved in water.

Leaf area

The isolated factor cultivars did not significantly influence the variables studied at the 0.01 and 0.05% probability level by the F test. However, the factor salinity levels of the nutrient solution influenced all the variables analyzed in this experiment. The mathematical fit that best fits the lettuce leaf area was the linear type (Figure 3). As the

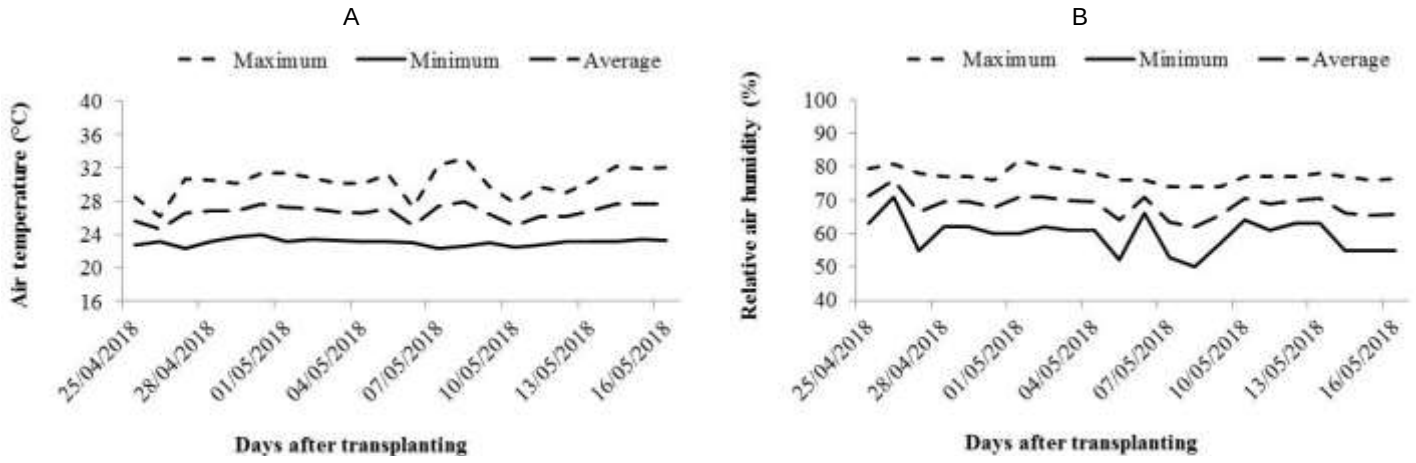

Figure 2. Temperature (A) and relative air humidity (B), maximum, minimum and average daily, observed during the period of conduction of the experiment.

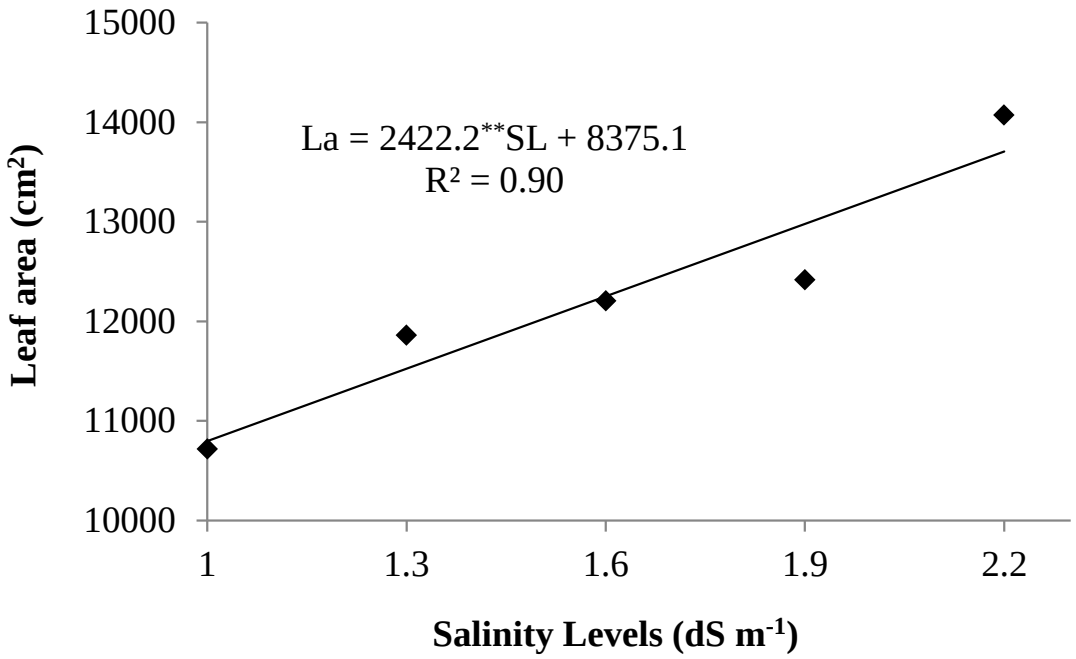

Figure 3. Averages of lettuce leaf area as a function of salinity levels of the nutrient solution.

salinity level of the nutrient solution increased, there was a positive increase in leaf area of lettuce, and the maximum yield was obtained in 2.2 dS m^{-1} of the nutrient solution, corresponding to 13703.94 cm² per plant. Magalhães et al. (2010), when evaluating different levels of water electrical conductivity in lettuce yield found satisfactory results for leaf area in the case of the electrical conductivity up to 3.0 dS m^{-1}. This is consistent with the results obtained in the present study.

The leaf area has great relevance for lettuce, since it is a growth variable indicative of leaf yield, and the photosynthetic process depends on the interception of the light energy and its conversion into chemical energy, a process that occurs directly on the leaf (Taiz and Zeiger, 2017). Cordeiro et al. (2017), when evaluating tolerance of lettuce cultivars to the saline water of the fish culture, observed that, in general, there was an increase in the leaf area with the increase of the salinity up to the levels of 2.48 and 2.83 dS m^{-1}; maximum leaf area values of 1,989.5 and 1,499.5 cm^2 per plant were observed, but these values are lower than those obtained in the present study, possibly because they are other lettuce cultivars.

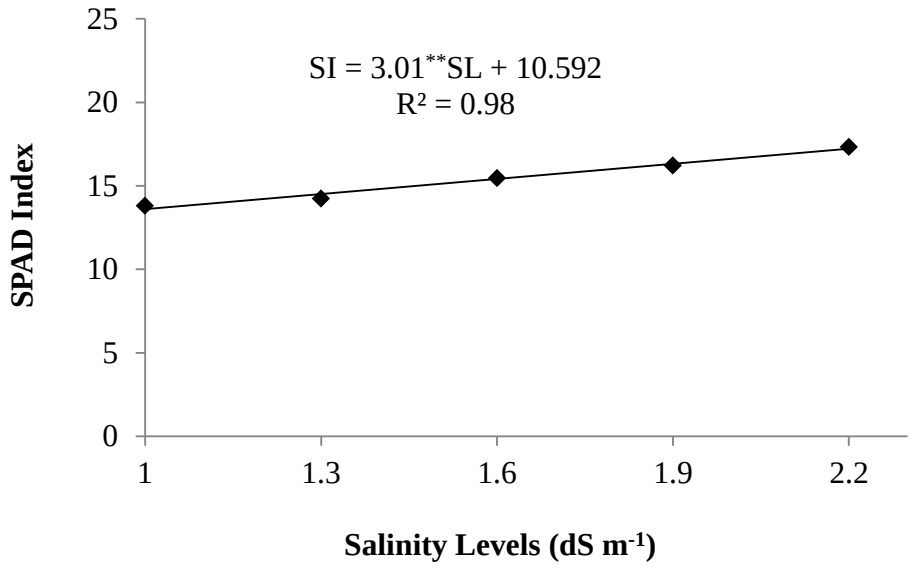

Figure 4. SPAD index as a function of the salinity levels of the nutrient solution.

SPAD index

Regarding the SPAD index, there was an increase when the salinity levels of the nutrient solution increased (Figure 4). Maximum SPAD yield was obtained in 2.2 dS m^{-1} of the nutrient solution, corresponding to 17.21. This fact can be related to a gradual effect provided by the water used to prepare the nutrient solution (rainwater 0.24 dS m^{-1}) and the short cycle of lettuce. This fact corroborates with the results of Soares et al. (2010), which showed an average SPAD index of 15.90, when submitted to different levels of salinity.

"a", "b" and total chlorophyll

The content of "a", "b" and total chlorophyll as a function of the electrical conductivity of the nutrient solution of the lettuce is shown in Figure 5. It is noted that the lowest concentration of chlorophyll was obtained in the treatment with 1.0 dS m^{-1}. It is observed in the figure that the levels of chlorophyll "a", chlorophyll "b" and total chlorophyll are increasing linearly as the salinity levels of the nutrient solution increase (Figures 4A, B and C).It is also noted that the highest concentration for chlorophyll a, b, and total was obtained with a salinity level of 2.2 dS m^{-1}, which are 0.55, 0.22 and 0.73 mg g^{-1} mf^{-1}.

Generally, photosynthetic pigments are adversely affected by saline stress, accelerating their degradation rapidly or reducing their biosynthesis (Ashraf and Harris, 2013). However, in this study the levels of "a", "b" and total chlorophylls increased significantly when salinity levels of the nutrient solution increased, a fact that is possibly related to the nutrients being supplied in a readily assimilable way by the culture. Sarmento et al. (2014), evaluating the use of salt rejected in the cultivation of hydroponic lettuce, also observed that the salinity of the nutritive solution raised the chlorophyll levels of the plants. Increased chlorophyll content in response to increased salinity was also observed by Paulus et al. (2010), who worked with two lettuce cultivars in hydroponics using different saline solutions and found an increase of chlorophyll under conditions of higher salinity.

Carotenoids

For the carotenoid variable, it was observed that the highest value was obtained with salinity of nutrient solution of 2.2 dS m^{-1}, corresponding to 0.13 mg g^{-1} mf^{-1} (Figure 6). Possibly, this fact occurred due to the higher nutritional supply for this level of salinity, since these salinity levels were established taking into consideration the application of fertilizers to water. These photosynthetic pigments known as carotenoids are derived from secondary metabolism, and have antioxidant activity; they act in the intercellular communication in the activity of the immune system providing the preventive capacity of diseases (Skibsted, 2012).

Vegetables are the major sources of carotenoids, including vitamin A precursors (Haskell, 2013). They are compounds classified as xanthophylls (lutein and zeaxanthin) and carotenes (α-carotene, β-carotene and lycopene) (Britton, 2008). The vegetables that have green color in their composition have different types of carotenoids, such as β-carotene, neoxanthin, lutein, violaxanthin and others. β –carotene and lutein are

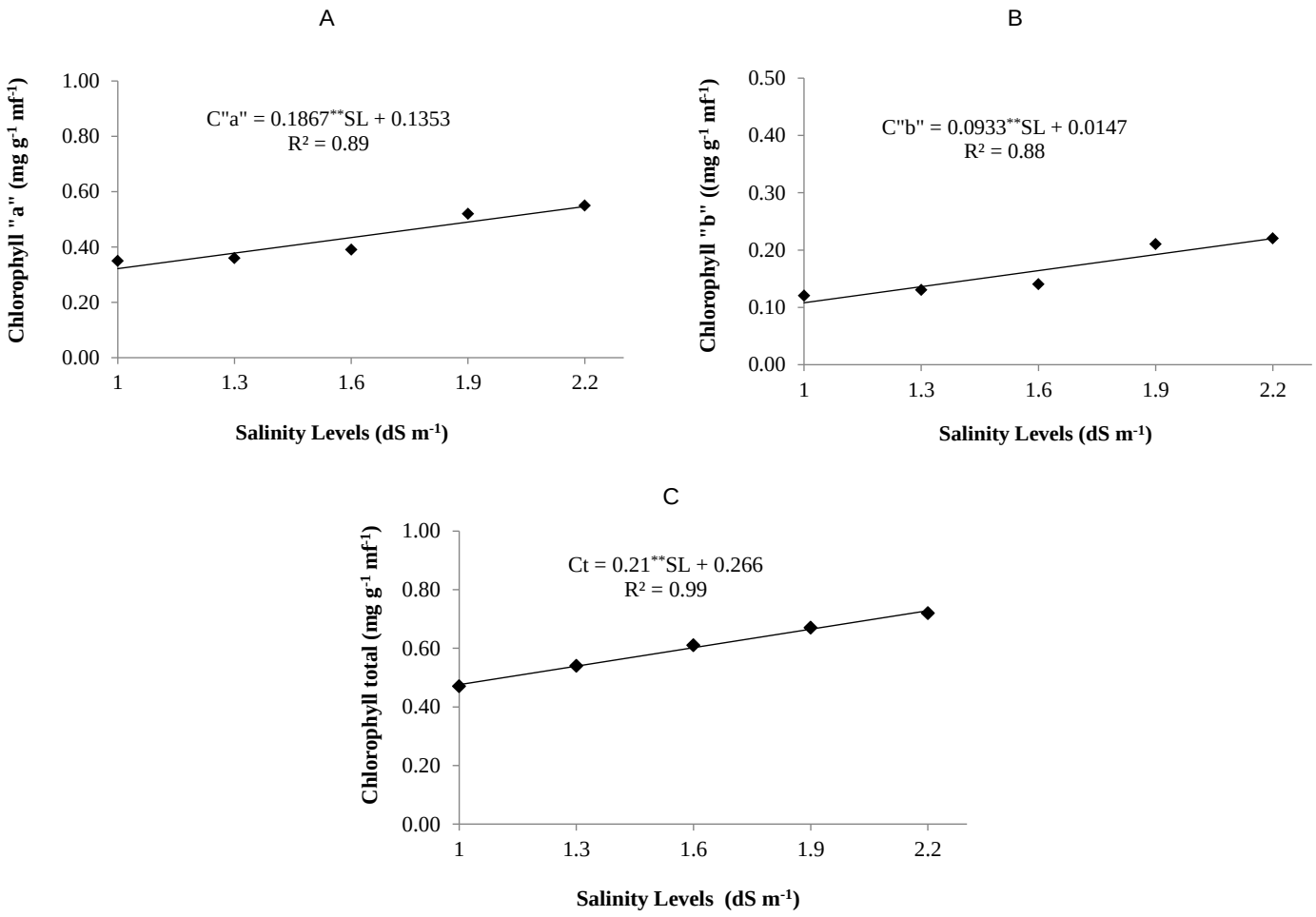

Figure 5. Chlorophyll a (A), b (B) and total (C) averages of lettuce as a function of salinity levels of the nutrient solution.

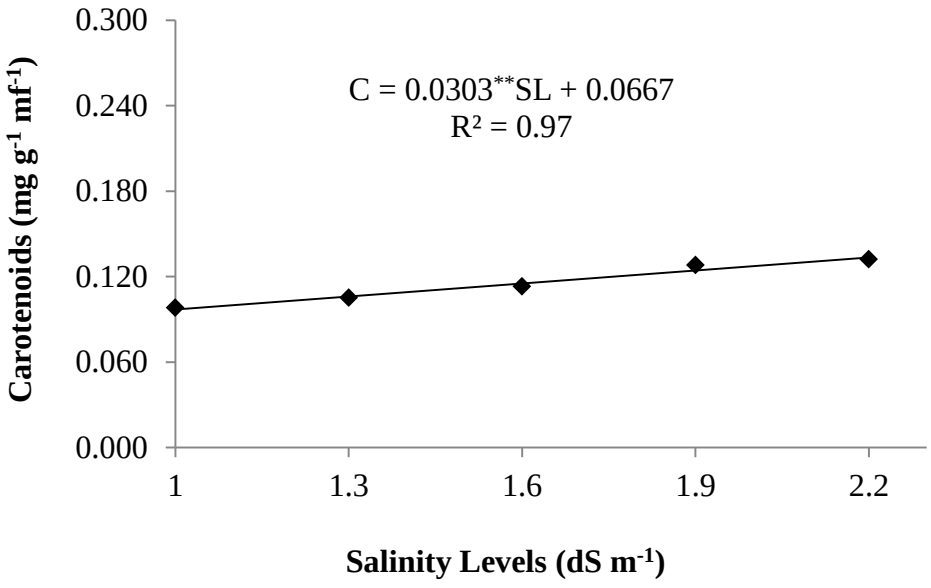

Figure 6. The carotenoids pigments averages of lettuce as a function of the salinity of the nutrient solution.

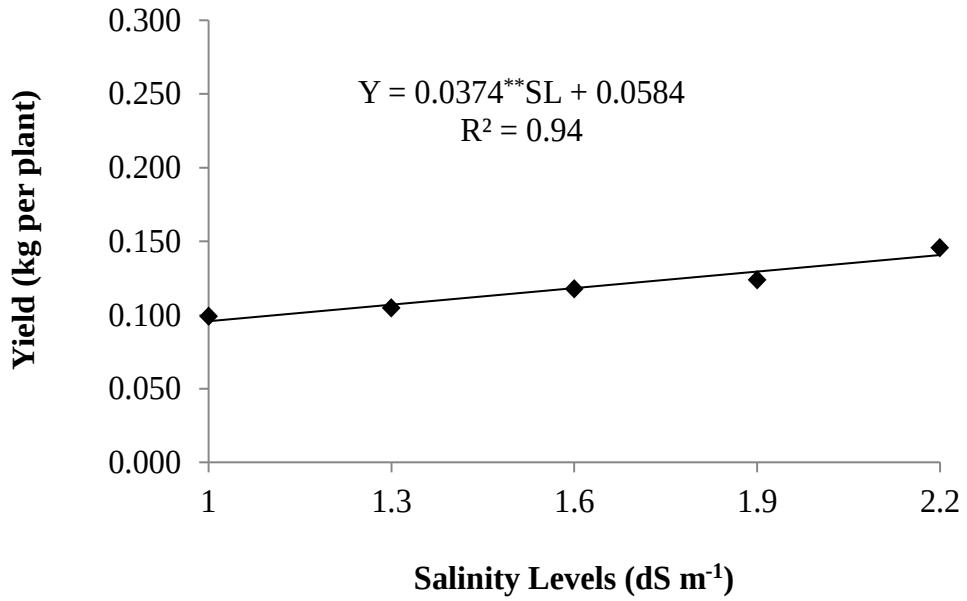

Figure 7. Average yield of lettuce leaves as a function of salinity levels of the nutrient solution.

considered the most important nutritional carotenoids (Wang et al., 2010), having a photoprotective and antioxidant action (Lee et al., 2013).

Yield

The mathematical model that best fit the yield of lettuce leaves in kg per plant at the end of the crop cycle was linear; it functioned as the salinity levels of the nutrient solution (Figure 7). It was observed that as the salinity level of the nutrient solution increased, there was a positive increase in the yield of lettuce leaves, and the maximum yield was obtained in 2.2 dS m^{-1} of the nutrient solution, corresponding to 0.140 kg per plant.

Vasconcelos et al. (2014) studied the development of coriander in salt solutions and observed that in the nutrient solution recommended by Castellane and Araújo (1994), the maximum yield estimated at the highest level of the nutrient solution, corresponding to 2.07 dS m^{-1}, and in the solution nutritional composition of Furlani et al. (1999), the estimated maximum yield in fresh matter was when the electrical conductivity (EC) of the nutrient solution was 1.63 dS m^{-1}. Results of other authors are similar to those obtained in the present study and, possibly, this fact is related to the salinity levels of the nutrient solution being based on the addition of fertilizing salts. Dias et al. (2011) found that salinity higher than 2.3 dS m^{-1} makes it difficult to produce leaves in hydroponic lettuce plants. Regarding salinity, the values observed in all treatments studied remained below this level and were not considered harmful to the development of the studied culture.

Conclusions

The isolated cultivar factor did not significantly influence any of the analyzed variables of the hydroponic lettuce. The different levels of salinity of the nutrient solution positively influenced the variables analyzed: leaf area, SPAD index, chlorophyll a, b and total, and yield of leaves of hydroponic lettuce. Hydroponic lettuce can be grown up to 2.2 dS m^{-1} of electrical conductivity of the nutrient solution without any loss in yield.

CONFLICT OF INTERESTS

The authors have not declared any conflict of interests.

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