Hydrogen peroxide as attenuator of salt stress effects on the physiology and biomass of yellow passion fruit


ABSTRACT: The success of yellow passion fruit cultivation in the semi-arid region of Northeast Brazil is conditioned on the ability of this crop to develop under salt stress conditions, so it is necessary to identify techniques capable of attenuating the deleterious effects caused by irrigation with high-salinity waters. In this context, the present study aimed to evaluate the fluorescence, photosynthetic pigments and biomass of yellow passion fruit cultivated under salt stress and foliar application of hydrogen peroxide. The study was conducted in a greenhouse, with the experimental design in randomized blocks with three replicates, in a 4 × 4 factorial scheme, which consisted of four values of irrigation water electrical conductivity - ECw (0.7, 1.4, 2.1 and 2.8 dS m⁻¹) and four concentrations of hydrogen peroxide (0, 20, 40 and 60 µM). Irrigation using water with ECw from 1.4 dS m⁻¹ compromised the photochemical efficiency, photosynthetic pigments and biomass production of yellow passion fruit. Application of hydrogen peroxide at concentration of 20 µM promoted the highest values for variable and maximum fluorescence and concentration of carotenoids, constituting an alternative for the acclimation of yellow passion fruit to salt stress. Application of hydrogen peroxide at concentrations above 20 µM intensified the salt stress on passion fruit.

Key words: Passiflora edulis f. flavicarpa Deneger, mitigating, salinity, physiology

HIGHLIGHTS:
- Electrical conductivity of water (ECw) higher than 0.7 dS m⁻¹ increases carotenoid concentration in yellow passion fruit.
- Dry biomass accumulation in yellow passion fruit is inhibited by ECw above 0.7 dS m⁻¹.
- H₂O₂ at concentration of 60 µM increases chlorophyll b concentration in yellow passion fruit when irrigated with water of 2.8 dS m⁻¹.

RESUMO: O sucesso do cultivo de maracujazeiro amarelo na região semiárida do Nordeste brasileiro está condicionado à capacidade da cultura em desenvolver-se sob condições de estresse salino, fazendo-se necessário identificar técnicas capazes de amenizar os efeitos deletérios ocasionados pela irrigação com águas de elevada salinidade. Neste contexto, objetivou-se avaliar a fluorescência, pigmentos fotossintéticos e biomassa de maracujazeiro amarelo cultivado sob estresse salino e aplicação foliar de peróxido de hidrogênio. A pesquisa foi conduzida em casa de vegetação, com o delineamento experimental de blocos casualizados com três repetições, em esquema fatorial 4 × 4, os quais consistiram de quatro valores de condutividade elétrica da água de irrigação - CEa (0.7; 1.4; 2.1 e 2.8 dS m⁻¹) e quatro concentrações de peróxido de hidrogênio (0, 20, 40 e 60 µM). A irrigação com água de CEa a partir de 1.4 dS m⁻¹ comprometeu a eficiência fotoquímica, os pigmentos fotossintéticos e a produção de fitomassa do maracujazeiro. A aplicação de peróxido de hidrogênio na concentração de 20 µM promoveu os maiores valores para fluorescência variável e máxima e conteúdo de carotenoides constituindo-se como alternativa para aclimatação do maracujazeiro ao estresse salino. A aplicação de peróxido de hidrogênio em concentração superior a 20 µM intensificou o estresse salino sobre o maracujazeiro.

Palavras-chave: Passiflora edulis f. flavicarpa Deneger, mitigação, salinidade, fisiologia
**Introduction**

Yellow passion fruit has high potential for production due to the great adaptation to soil and climatic conditions and the rapid return compared to other fruit species (Souza & Ribeiro, 2016). Passion fruit can be consumed fresh and/or processed through carbonated and mixed drinks, syrups, jellies, dairy products, ice cream, and canned foods (Santos et al., 2017). In the semi-arid region of Northeast Brazil, due to high evaporation rates and irregular rainfall, the availability of water for irrigation is reduced both in quantity and quality (Silva et al., 2021). Therefore, the expansion of irrigated cultivation of yellow passion fruit is conditioned on the use of water with high levels of salts. However, the use of saline water causes deleterious effects on crops, and yellow passion fruit is considered sensitive to salinity (Pinheiro et al., 2022), with decrease in growth from 0.3 dS m⁻¹ in irrigation water (Lima et al., 2021).

An alternative aiming at inducing acclimation of plants to salt stress that has recently gained prominence is the exogenous application of hydrogen peroxide, which at adequate concentrations has an intracellular signaling function to activate stress responses (Veloso et al., 2022). Pre-exposure of plants to signaling metabolites such as H₂O₂ increased transpiration and CO₂ assimilation rate in *Passiflora edulis* f. *flavicarpa* Deneger (Silva et al., 2019a), stomatal conductance, chlorophyll a, b, and total biosynthesis, and chlorophyll fluorescence in *Annona muricata* L. (Silva et al., 2019b; Veloso et al., 2021).

In this context, the present study aimed to evaluate the fluorescence, photosynthetic pigments, and biomass of yellow passion fruit cultivated under salt stress and foliar application of different concentrations of hydrogen peroxide.

**Material and Methods**

The study was conducted in drainage lysimeters under greenhouse conditions, at the Center of Technology and Natural Resources (CTRN) of the Federal University of Campina Grande (UFGC), located in the municipality of Campina Grande, PB, Brazil, situated by the local geographic coordinates 7° 15’ 18” S latitude S, 35° 52’ 28” W longitude and an average altitude of 550 m. The data of maximum and minimum temperature and relative humidity of the air during the experimental period are presented in Figure 1.

The experimental design was in randomized blocks in a 4 × 4 factorial arrangement. The treatments resulted from the combination of four values of irrigation water electrical conductivity - ECw (0.7; 1.4; 2.1 and 2.8 dS m⁻¹) and four concentrations of hydrogen peroxide (0; 20; 40 and 60 µM), The experimental unit consisted of one plant. Hydrogen peroxide concentrations were defined based on results obtained by Silva et al. (2019a).

The solutions with different water salinity levels were prepared by dissolving the salts NaCl, CaCl₂.2H₂O, and MgCl₂.6H₂O, at an equivalent proportion of 7:2:1, which prevails in sources of water commonly used for irrigation in small properties of the Northeast region, adjusting their concentrations using the available supply water. The quantities of salts were determined considering the relationship between ECw and the salt concentration (Richards, 1954), according to Eq. 1:

\[
Q = 10 \times ECw
\]

(1)

where:

- Q - quantity of salts to be added (mmol L⁻¹); and,
- ECw - electrical conductivity of water (dS m⁻¹).

After preparation and calibration of ECw values, using a portable conductivity meter, the waters were stored in 200 L plastic pots, one for each ECw value, properly protected to avoid evaporation and contamination with materials that may compromise their quality. The different concentrations of hydrogen peroxide were applied by foliar spraying, performed at 15-day intervals (Silva et al., 2019b), until the beginning of flowering, using a backpack sprayer.

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**Figure 1.** Air temperature (maximum and minimum) and relative air humidity during the experimental period
The experiment used seeds of the yellow passion fruit variety commonly known as ‘Guinezinho’, traditionally cultivated in the municipalities of Cuité, in the state of Paraíba, and Jaçanã, in the state of Rio Grande do Norte. These seeds were collected from fruits of a commercial orchard, extracted from plants subjected to the mass selection in the municipality of Nova Floresta, and standardized based on vigor and health.

The seedlings were produced sexually (seeds) in citropote® with capacity of 6 dm³, filled with substrate, composed of a mixture (v/v) of 84% soil, 15% washed sand, and 1% organic compost (earthworm humus) until reaching 5.6 dm³ of volume (Andrade et al., 2019).

At 65 days after sowing, when the main stem was approximately 35 cm long, the plants were transplanted to 100 L pots adapted as drainage lysimeters, filled with a 0.5-kg layer of crushed stone, followed by 100 kg of properly pounded Entisol of sandy loam texture (0-20 cm depth), from the rural area of the municipality of Lagoa Seca, PB, Brazil, whose chemical and physical characteristics were determined according to the methodologies proposed by Teixeira et al. (2017): Ca²⁺, Mg²⁺, Na⁺, K⁺, H⁺ + Al³⁺ = 2.60, 3.66, 0.16, 0.22 and 1.93 cmol kg⁻¹, respectively; exchangeable sodium percentage = 1.87%; organic matter = 1.36 dag kg⁻¹; P = 6.80 mg kg⁻¹; electrical conductivity of the saturation extract = 1.0 dS m⁻¹; and pH in water (1:2.5) = 5.90; sand, silt and clay = 732.90, 142.10 and 125.0 g kg⁻¹, respectively; apparent and particle density = 1.39 and 2.66 kg dm⁻³, respectively.

Each lysimeter, perforated at the base to allow drainage, was connected to a 16-mm-diameter transparent drain. The tip of the drain inside the lysimeter was involved with a nonwoven geotextile (Bidim OP 30) to avoid clogging by soil material. A plastic bottle was placed below each drain to collect the drained water and estimate the water consumed by the plant during the interval by water balance.

The water volume required for the soil to reach field capacity was determined before transplanting, applying water according to the established treatments. After transplanting, irrigation was performed daily at 17 hours, applying in each lysimeter the estimated water volume according to each treatment to maintain the soil moisture close to field capacity and avoid the accumulation of salts in the soil. The volume of water to be applied was determined according to the water requirement of the plants, estimated by water balance: volume applied minus volume drained in the previous irrigation, plus a leaching fraction of 0.15.

In the cultivation, spacing of 1.50 m between rows and 2.20 m between lysimeters was established, using the trellis system with wire n° 14, installed inside the greenhouse, at 2.40 m height from the floor and 1.60 m height from the soil in the lysimeter. Formative pruning and phytosanitary control were similar to those described in the study of Andrade et al. (2019). As the experiment was conducted in a greenhouse, pollination was performed artificially (between 12:00 and 15:00 hours).

Fertilization was performed according to the recommendation of Sáo José et al. (2000), applying 250 g of single superphosphate and 100 g of potassium chloride (60% K₂O), and 150 g of single superphosphate (P₂O₅ = 18%; Ca²⁺ = 16% and S = 10%) per plant as top-dressing at the beginning of flowering (116 days after transplanting - DAT). Fertilization with nitrogen and potassium was performed monthly, also as top-dressing, according to the recommendation of Santos (2001), using ammonium sulfate (N = 20%; S = 22%) and potassium chloride as sources of nitrogen and potassium. In the vegetative stage of the crop, the N:K ratio was used, considering the quantity of 10 g of nitrogen as reference. From the beginning of flowering, the N dose was elevated to 20 g and the K dose to 30 g, increasing the N:K ratio to 1:1.5.

The effects of treatment on the yellow passion fruit crop were determined at 186 DAT, period of full flowering and beginning of fruit formation, through the measurements of chlorophyll a fluorescence, photosynthetic pigments: chlorophyll a (Chl a), chlorophyll b (Chl b), carotenoids (Car), leaf dry biomass (LDB), stem dry biomass (StDB) and shoot dry biomass (ShDB). Chlorophyll a fluorescence was measured by determining the initial fluorescence (F₀), maximum fluorescence (Fm), variable fluorescence (Fv), and the potential quantum efficiency (Fv/Fm) in leaves pre-adapted to the dark using leaf clips for 30 min, between 7:00 and 8:00 a.m., in the middle leaf of the intermediate productive branch of the plant, using the modulated fluorometer Plant Efficiency Analyser - PEA II.

Chlorophyll a, chlorophyll b, and carotenoid concentrations were determined following the method developed by Arnon (1949), using samples of five discs from the blade of the third mature leaf from the apex. The values obtained for the concentrations of chlorophyll a, chlorophyll b, and carotenoids in the leaves were expressed in mg g⁻¹ of fresh matter (mg g⁻¹ FM).

To evaluate the dry biomass accumulation in the leaf (LDB), stem (StDB) and shoot (ShDB) of the yellow passion fruit plants, the stem of each plant was cut close to the soil at 205 DAT and subsequently dried in a forced ventilation oven at 65 °C until constant weight. Then, the material was weighed to obtain the values expressed in g per plant.

The data collected were subjected to analysis of variance at p ≤ 0.05 and, when significant, polynomial regression analysis (p ≤ 0.05) was performed using the statistical program SISVAR (Ferreira, 2019).

**Results and Discussion**

According to the result of the F test (Table 1), all variables analyzed were significantly affected (p ≤ 0.05) by irrigation water electrical conductivity. Regarding the hydrogen peroxide concentrations, significant differences were observed in variable fluorescence (Fv) and maximum fluorescence (Fm) of chlorophyll a, in addition to the photochemical efficiency of PSII (Fv/Fm) and carotenoids (Car). The interaction between the factors significantly affected only the chlorophyll b concentrations.

According to the estimate obtained through the regression equations (Figures 2A), yellow passion fruit plants when subjected to ECw of 2.8 dS m⁻¹ showed a 20.46% increase in the initial fluorescence compared to plants irrigated with water of lowest electrical conductivity (0.7 dS m⁻¹). The results

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Table 1. Summary of F test for initial fluorescence (F₀), variable fluorescence (Fᵥ), maximum fluorescence (Fₘ), the quantum efficiency of PSII (Fᵥ/Fₘ), chlorophyll a (Chl a), chlorophyll b (Chl b), carotenoids (Car), at 186 days after transplanting (DAT) and leaf dry biomass (LDB), stem dry biomass (StDB), and shoot dry biomass (ShDB), at 205 DAT of yellow passion fruit under saline water irrigation and exogenous application of hydrogen peroxide (H₂O₂).

<table>
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<th>Source of variation</th>
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<td>Salinity levels (SL)</td>
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<td>Linear regression</td>
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<td>Hydrogen peroxide (H₂O₂)</td>
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<td>Interaction (SL × H₂O₂)</td>
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*- Respectively not significant, significant at p ≤ 0.01 and p ≤ 0.05 by F test.

Figure 2. Initial fluorescence - F₀ (A) and variable fluorescence - Fᵥ (B) of yellow passion fruit, as a function of electrical conductivity of water - ECw; and variable fluorescence - Fᵥ (C) as a function of the hydrogen peroxide concentrations - H₂O₂ obtained for F₀ suggest that the ECw values studied caused damage to the photosynthetic apparatus of the passion fruit plants, compromising the PSII, because plants subjected to stress tend to increase their initial fluorescence. This situation is indicative of damage to the light-harvesting complex (LHCII), which is responsible for transferring excitation energy to the PSII reaction center, or even a separation between the reaction center and the LHCII (Cruz et al., 2009).

The variable fluorescence of yellow passion fruit plants also decreased linearly as a function of the increase in ECw levels (Figure 2B), whose decrease was 5.39% per unit increase in ECw. When comparing the Fᵥ of plants cultivated under ECw of 2.8 dS m⁻¹ to those irrigated with water of 0.7 dS m⁻¹, there was a decrease of 11.77%. Fᵥ is associated with the ability to transfer energy from electrons ejected from pigment molecules to the formation of the reductant NADPH, ATP and reduced ferredoxin (Baker, 2008). Thus, the decline in electron transport and ATP and NADPH production inhibits the photosynthetic process, given that these compounds are essential for CO₂ fixation in the Calvin cycle. When subjecting yellow passion fruit to salt stress (ECw = 4.5 dS m⁻¹), as in the present study, Freire et al. (2014) observed a 9.6% reduction in the Fᵥ of plants subjected to irrigation with saline water. These authors attributed such a reduction to the occurrence of damage to the PSII of the passion fruit plants.

Exogenous application of hydrogen peroxide significantly (p ≤ 0.05) affected the Fᵥ of yellow passion fruit and, as observed in Figure 2C, the data were described by a quadratic model. Through the regression equation (Figure 2C), it can be observed that the maximum estimated value for Fᵥ (386.52) was obtained when the passion fruit plants were subjected to H₂O₂ concentration of 20.8 µM. When plants subjected to 20 µM were compared to those which received H₂O₂ concentrations of 0 and 60 µM, there were reductions of 4.44 and 15.75% in Fᵥ, respectively. Thus, it can be inferred that the increase in Fᵥ promoted by the application of 20 µM of H₂O₂ is indicative of the efficiency of this concentration in the acclimation of passion fruit plants. Hydrogen peroxide can trigger the activation of defense mechanisms in plants, including increased levels of antioxidants, reducing damage to the ultrastructure of mesophyll cells caused by salt stress. It can also increase leaf chlorophyll concentrations, fluorescence variables, and soluble carbohydrate and protein concentrations (Hossain et al., 2015).
Hydrogen peroxide as attenuator of salt stress effects on the physiology and biomass of yellow passion fruit

The quantum yield of photosystem II in yellow passion fruit plants was significantly and negatively influenced by ECw (Table 1). According to the regression equation (Figure 4A), the salt stress caused linear reduction of 6.36% in Fv/Fm per unit increase in ECw, i.e., the Fv/Fm decreased from 0.76 to 0.65, which corresponds to 13.98%, between yellow passion fruit plants subjected to ECw of 2.8 dS m⁻¹ and those cultivated under the lowest ECw (0.7 dS m⁻¹). The decrease in the quantum yield of photosystem II indicates the occurrence of the photoinhibitory effect caused by salt stress (Cruz et al., 2014) and implies that the photosynthetic efficiency of the leaves under ambient light conditions was compromised (Baker, 2008). Hence, the reduction observed in the quantum yield of photosystem II (P680) may be related to the increase in lipid peroxidation, as a result of the diversion of the electron flow from CO₂ assimilation to O₂ reduction (Cruz et al., 2009).

As verified for Fv and Fm, the increase in H₂O₂ concentrations also caused reductions in the Fv/Fm ratio and, according to the regression equation (Figure 4B), the quantum efficiency of PSII ranged from 0.75 to 0.67, resulting in reduction of 11.09%, between plants that did not receive the foliar application of H₂O₂ and those subjected to 60 µM. The reduction in Fv/Fm ratio with the increase in the H₂O₂ concentrations suggests that the increment of this reactive oxygen species (ROS) in plant tissues causes deleterious effects on the integrity of the photosynthetic apparatus of yellow passion fruit plants. According to Melo et al. (2017), increments in F₀ values associated with reduction in maximum fluorescence, as evidenced in this study, is indicative of damage to the light-harvesting complex, a situation that affects the transport of electrons to the PSII reaction center. In addition, the reduction in Fv and Fm is directly related to chlorophyll degradation (Dias et al., 2019). According to Melo et al. (2017), the decrease in chlorophyll a concentration with the increase in the electrical conductivity occurs due to osmotic and ionic toxicity effects.

Regarding the effect of hydrogen peroxide concentrations on the maximum fluorescence of yellow passion fruit plants, the Fm increased up to the concentration of 20 µM (Figure 3B), with maximum estimated value of 508.60, and decreased from this level on, reaching a minimum value of 465.72 in plants cultivated under 60 µM. Thus, it can be inferred that high concentrations of H₂O₂ can intensify the deleterious effects of the stress caused by high ECw on the yellow passion fruit crop.

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photosynthetic apparatus of the crop under study. Hydrogen peroxide is moderately reactive, has a long cellular half-life, and can move freely through the characteristic membranes, which allows this radical to induce processes such as stomatal closure and enzyme inactivation, in addition to causing damage to nucleic acids, proteins, and lipids (Gill & Tuteja, 2010).

According to Figure 5A, the increase in the ECw decreased the chlorophyll a content of yellow passion fruit by 17.38% per unit increase in electrical conductivity of water, i.e., in yellow passion fruit plants irrigated with ECw of 2.8 dS m\(^{-1}\) the chlorophyll a concentration was reduced by 41.54% compared to plants under the lowest value of ECw (0.7 dS m\(^{-1}\)). The degradation of photosynthetic pigments in plants grown under water salinity is probably a consequence of increased toxic ions, increased activity of the chlorophyllase enzyme, and damage to the photosynthetic apparatus (Trifunovic-Momcilov et al., 2021). As noted by Lima et al. (2020), the increase in ECw from 0.3 to 3.5 dS m\(^{-1}\) led to reduction in the Chl a concentrations of yellow passion fruit plants.

Chlorophyll b concentrations of yellow passion fruit plants were significantly affected by the interaction between ECw and H\(_2\)O\(_2\) levels (Figure 5B). Plants grown under ECw of 2.8 dS m\(^{-1}\) obtained the maximum value of Chl b (0.975 mg g\(^{-1}\) FM) under foliar application of 60 µM. However, the use of water with electrical conductivity of 0.7 dS m\(^{-1}\) and the absence of H\(_2\)O\(_2\) (0 µM) resulted in the lowest Chl b value (0.320 mg g\(^{-1}\) FM). Chl a is the “converter” and the center of reaction of optical energy, besides absorbing light, whereas Chl b only acts on the absorption of optical energy (Zhang et al., 2013). The capture of excess light energy induces the reorganization of the photosynthetic apparatus to optimize light absorption, preventing photo-oxidative damage (Borisova-Mubarakshina et al., 2015).

The concentration of carotenoids in yellow passion fruit leaves increased linearly with the increment in ECw values and, according to the regression equation (Figure 6A), there was increment of 76.52% per unit increase in ECw, which corresponded to increment of 104.64% in plants under the highest values of ECw compared to those irrigated using water with the lowest electrical conductivity. Increased production of carotenoids is possibly linked to mechanisms of protection of the photosynthetic apparatus, aimed at preventing photoinhibition under stress conditions, besides reflecting acclimation response of the plants, because these pigments can act as antioxidant agents, which protect lipid membranes from oxidative stress when plants are subjected to salt stress (Falk & Munné-Bosch, 2010).

The carotenoid concentrations obtained in the present study are lower than those observed by Lima et al. (2020) when they evaluated the chloroplast pigments of ‘BRS Rubi do Cerrado’ sour passion fruit under irrigation with water of different electrical conductivities (ECw varying from 0.3 to 3.5 dS m\(^{-1}\)), which showed increase in carotenoid concentration of 2.83 mg g\(^{-1}\) FM in plants irrigated with ECw of 3.5 dS m\(^{-1}\) in comparison to those cultivated under the lowest water salinity (0.3 dS m\(^{-1}\)). The divergence in the results obtained in these studies may be related to the evaluation period (40 DAS versus 186 DAT) and the genotype tested.

The carotenoid concentration in yellow passion fruit as a function of H\(_2\)O\(_2\) concentration was described by a quadratic regression model \(y = 0.5525x + 0.00235x^2 - 0.00006x^3\) \(R^2 = 0.54\) but the coefficient of determination was rather low for prognostic purposes.

Chlorophyll a concentration constitutes an important factor linked to photosynthetic efficiency (Fv/Fm) and, consequently, to plant growth (Dias et al., 2019). Thus, the reductions observed in the quantum efficiency of PSII (Figure 4A), as well as in the chlorophyll a content (Figure 5A) of yellow passion fruit plants subjected to salt stress, were expected to result in a decrease in biomass production. As can be seen, the data of leaf dry biomass (Figure 6B), stem dry biomass (Figure 6C), and shoot dry biomass (Figure 6D) decreased linearly in response to the increase in ECw and the reductions were of the order of 17.86, 14.11, and 16.11%, per unit increase in ECw, in LDB, StDB, and ShDB, respectively, i.e., the increase in water salinity level from 0.7 to 2.8 dS m\(^{-1}\) reduced leaf, stem, and shoot dry biomass by 113.63 g (42.87%), 78.77 g (32.87%), and 192.41 g (38.12%) of dry matter per plant, respectively. The reduction in biomass production may be related to the ionic and/or osmotic components of the salt stress, and the low availability.
For Santos et al. (2016), the effect of the increase in salt concentration decreases the shoots of plants, because they do not have an osmotic adjustment as a mechanism of adaptation to excess salts in the soil solution. Thus, it can be inferred that the irrigation of passion fruit using water with ECw above 1.4 dS m\(^{-1}\) compromises its growth, possibly because it cannot osmotically adjust to the different levels of salinity.

**Conclusions**

1. Irrigation using water with electrical conductivity above 1.4 dS m\(^{-1}\) decreases the photochemical efficiency, photosynthetic pigments, and biomass production of yellow passion fruit.

2. Application of hydrogen peroxide at a concentration of 20 µM promotes the highest values of variable and maximum fluorescence and concentration of carotenoids in passion fruit.

3. Hydrogen peroxide at a concentration of 60 µM stimulates the synthesis of chlorophyll b in plants irrigated with water of 2.8 dS m\(^{-1}\).

**Literature Cited**


