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Translocation of photoassimilates in melon vines and fruits under salinity using ^{13}C isotope

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ABSTRACT

Both yield and quality of Cantaloupe melon in semi-arid regions are threatened by high levels of salinity in irrigation waters. Our study aimed to characterize the translocation of photoassimilates in melon plants cultivated under salinity condition, using carbon 13 ($^{13}CO_2$) isotopic enrichment. Plants of the melon hybrid 'Zielo' were cultivated and drip-irrigated with waters of electrical conductivity (ECw) of 0.5 and 3.5 dS m^{-1}. Leaves were evaluated for concentrations of Na, Cl, and sucrose and their CO_2 assimilation rate. Fruits were evaluated for their weight, yield, sucrose, and soluble solids. Salinity stress affected both assimilation and accumulation of sugars, decreased fruit number and size. The natural (before enrichment) and enriched ^{13}C in leaves from three stem regions and fruits were evaluated in the two final weeks of the crop cycle. The isotopic enrichment was applied to leaves of the basal and apical regions of the primary stem and apical leaves of the secondary stem. Although Na and Cl accumulated in all leaves, accumulation was the highest in basal leaves, causing a significant reduction of net assimilation of CO_2 in these leaves. Although salinity significantly reduced fruit numbers and weight, it did not affect fruit soluble solids. Under saline conditions, leaves had a greater isotopic preference for the fixation of ^{13}C than ^{12}C. Two weeks before fruit harvest, regardless of salinity, fruits were the preferential sinks for carbon originated from leaves from the basal and apical parts of the stem. During fruit harvest week, basal and apical leaves of plants irrigated with water of ECw =0.5 dS m^{-1} had little or no ^{13}C contribution to the fruit, whereas leaves (mainly basal) of plants irrigated with ECw =3.5 dS m^{-1} continued to send photoassimilates to the fruit. Thus, saline stress reduced fruit size and number significantly and delayed carbon translocation to fruits, delaying fruit maturation. Results suggest that under saline stress, eliminating fertigation two weeks before fruit harvest to reduce fertilizer costs may not be beneficial to melon producers. However, fertigation can be stopped in the last week before harvest when using low-salinity water. Further studies are needed to determine if extending the crop cycle under salinity may compensate for delayed fruit maturation and increase fruit sugars.

1. Introduction

The world production of melon was 27.35 million tons in 2018 (FAO – Food and Agriculture Organization (2018)). Melon plants are adapted to various agronomic conditions, and found in different regions including the Mediterranean, Central and Eastern Asia, America, as well as Central and southern Africa (Endl et al., 2018). In Brazil, melon is cultivated mainly in the Northeast semi-arid region, which has limited fresh water supply. In this region, as in other semi-arid regions of the world, producers must manage the crop in ways that try to mitigate the deleterious effects of salinity on fruit yield and quality.

Salinity is an abiotic stress that severely limits the growth and productivity of crops (Munns and Tester, 2008) due to nutritional imbalance, change in metabolic processes, disorganization of chloroplast, and reduction in cell division and expansion (Zhu, 2001). Salt stress also increases the production of reactive oxygen species (ROS) (Sharma et al.,

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2012). Since both photosynthesis and cell growth are among the primary processes affected by abiotic stress (Chaves et al., 2009), there is a reduction in both the assimilation and metabolism of carbon and in the accumulation of sugars, thus affecting mainly fruit yield and quality (Poljakoff-Mayber and Lerner, 1994).

Salt stress can lead to the total or partial closure of stomates, reducing CO_2 assimilation and, consequently, plant growth. Plants assimilate atmospheric CO_2 and reduce the level of triose-phosphate during photosynthesis, which can then be used to produce more complex carbohydrates, mainly sucrose and starch. Practically all production of biomass depends on carbohydrates produced during photosynthesis (Taiz and Zeiger, 2013).

In young active developing organs (sink), transported sugars are either consumed during growth or stored as reserve (Pierre et al., 2010). The transport of photoassimilates through the phloem is performed predominantly in the form of sucrose or compounds derived from raffinose and stachyose. In melon plants, sucrose, raffinose, and stachyose are the major carbohydrates translocated in the phloem (Chrost and Schmitz, 1997). As fruits do not accumulate storage carbohydrates (starch), the increase in their sucrose content depends on the translocation of carbohydrates produced in leaves (Hubbard et al., 1989).

Soluble sugars, which contribute with 65 % to 85 % of the fruit soluble solids, depends on the mechanisms of translocation of photoassimilates from leaves and their sequestration in fruits (Chitarra and Chitarra, 2005). Thus, it is necessary that these assimilates be efficiently transported to fruits, even in competition with other sinks such as other vegetative organs (Peil and Gálvez, 2005). Characterizing this sugar transport mechanism for fruits is a necessary step in trying to solve the problem of both low fruit weight, and number; consequently, low yield under saline conditions.

The flexibility of carbon partitioning in plants is fundamental to understand the production of primary metabolites and for plant response to environmental changes. Thus, understanding how plants adapt to changes in resource availability is linked to the mechanisms governing carbon allocation. The use of "tracers", notably ^{13}C, (a stable isotope of C), is a well-established approach to study translocation, allocation, carbon balance, and source-sink relations (Sulzman, 2007).

Kriedemann (1969) used carbon isotopic enrichment in lemon plants and reported that leaves only became efficient exporters of photoassimilates when they reached full maturity. The author noted that, after the appearance of strong sinks located in the apical stem region, the direction of photoassimilate translocation changed from basipetal (from top to bottom) to bidirectional. The author also concluded that the mature leaves did not receive photoassimilates.

Lai et al. (1988), studying patterns of assimilate transport from leaves to fruit in kiwifruit (*Actinidia deliciosa*), stated that photoassimilates produced by enriched leaves were directed preferentially to internodes, regardless of their location in the plant. The authors also observed that not all leaves located above the enriched leaf (n) received photoassimilates, that were distributed according to a phylaxic order n + 3, n + 5, and n + 8.

Finazzo et al. (1994) reported that most of the photoassimilates (98 %) produced by the enriched leaf, during the vegetative stage, were imported by leaves aligned in the same orthotic position (50 %), and by leaves adjacent to the enriched leaf (48 %). But, during the reproductive stage, photoassimilates produced in the enriched leaf were almost entirely (94 %) imported by fruits that were in the same orthotic alignment and, when there was no fruit in the enriched leaf alignment, the photoassimilates were distributed to the smaller fruits of adjacent alignments.

Vasconcellos (2001) evaluated photoassimilate partitioning in sweet passion fruit and observed that, during the vegetative stage, the apical meristem and leaves that had reached up to 60 % of their total size were the preferred sinks of assimilates exported from enriched leaves. When flower buds and fruits appeared, the preference for photoassimilate translocation changed and these organs became the strongest sinks.

Zhang et al. (2005) reported that the proportion of ^{13}C allocated to pear fruits at harvest varied with the enrichment time but increased as fruits grew. These authors showed that the amount and proportion of ^{13}C allocated to fruit were cultivar-dependent and could be mainly ascribed to differences in leaf growth, photosynthetic ability, and source strength among cultivars.

Bagues et al. (2018), analyzing the carbon isotope discrimination in two barley landraces under deficit irrigation with saline water, noted that deficient irrigation with saline water resulted in a decrease in $\Delta^{13}C$, indicating that the imposition of such stress led to less discrimination against the heavier isotope. Borzouei et al. (2020), analyzing effects of salt and nitrogen on physiological indices and carbon isotope discrimination of wheat cultivars, concluded that carbon isotope discrimination might be applicable as a useful tool for the study of salt-tolerance.

Studies involving carbon allocation and sequestration in melon plants under salinity stress are scarce. Thus, the objectives of this study were to apply the isotopic enrichment technique with $^{13}CO_2$ to characterize the translocation of photoassimilates in 'Cantaloupe' melon plants during the last two weeks of the crop cycle, and to evaluate the effect of irrigation with saline water on fruit size, number, and quality.

2. Material and methods

2.1. Location, soil and climate conditions

The field experiment was conducted from September to November 2016 at the Pacajus Experimental Station (Embrapa Agroindústria Tropical), located at 4°10′ S, 38°27′ W at an altitude of 60 m, Ceará State, Brazil. The soil was classified as a Typic Quartzipisamment (Quartz Sand) and its characteristics are reported in Table 1. The climate was classified as BSh of the Köppen's classification (Köppen, 1936), designated as a semi-arid climate. The climatic parameters: maximum and minimum temperatures, relative humidity, wind speed at 2 m height, and net radiation at the crop surface were evaluated through an automated weather station (**Suppl.** Fig. 1A).

2.2. Plant material, management, and treatments

Hybrid cantaloupe melon seedlings 'Zielo' purchased from Nunhems USA (Parma, USA) were obtained by sowing seeds into 200-cell polypropylene trays containing commercial substrate (Forth Flower Conditioner) from Forth Jardim (São Paulo, Brazil), with a cation exchange capacity (CEC) of 23 $cmol_c\,kg^{-1}$. Seedlings were acclimated in a greenhouse with misting and then transplanted to the experimental area 14 days after sowing when plants had two true leaves.

The soil of the experimental area had its base saturation increased by application of dolomitic limestone three weeks before planting, raising it from 62 to 80 %. After liming, the soil received two light diskings, raising cultivation beds 0.8 m W x21 m L and with 2.0 m spacing between beds. A drip irrigation system was installed with one drip line per bed, and beds were covered with double-face black/silver plastic mulch, silver side up. Seedlings were spaced every 0.8 m in the line.

Irrigation waters were delivered to plants through pressure-compensated Katif® drippers from Rivulis (Minas Gerais, Brazil) with a flow rate of 5.0 L h^{-1}, spaced every 0.8 m to provide one dripper per plant. The water distribution efficiency was evaluated using the coefficient of uniformity of Keller and Karmeli (1975) with a measured value of 95.5 %.

Crop water requirement was calculated from the IrrigaMelão spreadsheet, provided by Embrapa Tropical Agroindustry (EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária (2005)), using data collected in an automated weather station to determine the reference evapotranspiration (ET_0) (**Suppl.** Fig. 1B) according to Penman-Monteith methodology (Allen et al., 1998). Crop evapotranspiration (ETc) (**Suppl.** Fig. 1B) was determined by multiplying the ET_0 by the Kc. The total daily irrigation required and the irrigation time was

Table 1
Soil Characteristics.

Depth 0.0–0.3 m	Ca^{2+}	Mg^{2+}	Na^{+}	K^{+}	Al^{3+}	H + Al	SB	CEC
	……cmol$_c$ kg^{-1}……							
	1.03	0.83	0.33	0.26	0.0	1.49	2.45	3.93
	BS	ESP	P	OM	EC	pH	BD	
	……%……..		mg dm^{-3}	g Kg^{-1}	dS m^{-1}	H_2O	g cm^{-3}	
	62.0	8.4	12.1	11.5	0.54	6.0	1.76	

SB: Sum of bases; CEC: Cation exchange capacity; BS: Base saturation; ESP: Exchangeable sodium percentage; OM: Organic matter; EC: Electrical conductivity; and BD: Bulk density.

calculeted automatically by IrrigaMelão spreadsheet (EMBRAPA - Empresa Brasileira de Pesquisa Agropecuária (2005)).

Plants were fertilized by soil application and by fertigation. The nutrients applied through fertigation followed the Embrapa Melon Production System (EMBRAPA – Empresa Brasileira de Pesquisa Agropecuária (2016)) based on the soil analysis obtained from the Embrapa's Soil Laboratory (Table 1). The bed base fertilization consisted of 120 kg ha^{-1} of phosphorus as single superphosphate, 250 kg ha^{-1} of FTE BR-12 as a source of micronutrients and 20 m^3 ha^{-1} of cow manure. Fertigation was applied three times a week, from a nutrient stock prepared in a 20 L container and by a Venturi injector in a bypass system. The nutrients used in the fertigation were 120 kg ha^{-1} of nitrogen as urea and 80 kg ha^{-1} of potassium as potassium nitrate. These fertilizers were applied from transplanting to two weeks before harvest.

The treatments consisted of two different irrigation water electric conductivites (ECw) consisting of a control irrigation water of low salinity (ECw =0.5 dS m^{-1}) and a water of moderate salinity (ECw =3.5 dS m^{-1}) referred to as saline water. Each EC treatment consisted of eight irrigation lines representing the four replicates, two lines per replicate. To obtain ECw =3.5 dS m^{-1} from the 0.5 dS m^{-1} water we added sodium chloride (NaCl), considering that each 10 mM increase of NaCl corresponds to approximately 1 dS m^{-1} increase in EC; this was confirmed and monitored by a conductivity meter, model CD-4301 from Lutron (Taipei, TW).

2.3. Carbon assimilation rate, inorganic and organic compounds, and enrichment parameters

Leaf and fruit were sampled during the two weeks corresponding to the isotopic enrichment (two weeks before harvest and during harvest week). For the leaf analysis, the primary and secondary stems were sampled for leaves from the basal, middle and apical regions.

The CO_2 assimilation rate – photosynthesis (A, in μmol m^{-2} s^{-1}) was performed with an infrared gas analyzer IRGA from LCpro ADC (Hoddesdon, UK). Sodium (Na), chloride (Cl), and sucrose (Suc) concentration in leaves were analyzed from an extract of 1 g of ground lyophilized samples suspended in 20 mL using filtered deionized water (milli-Q system) from Millipore Corporation (Massachusetts, USA).

Sodium (Na) was analyzed by flame photometry. Chloride (Cl) was determined by spectrometry, first by mixing 3 mL of diluted extract with 0.5 mL of $Hg(SCN)_2$ in absolute methanol, and $Fe(NO_3)_3.9H_2O$ in deionized water. After mixing, the chloride was measured by absorbance readings at a wavelength of 460 nm in a spectrophotometer 15 min after the homogenization of the mixture. Chloride concentrations were determined using a standard NaCl curve (Gaines et al., 1984). Sucrose was determined in leaves and fruits by high-performance liquid chromatography (HPLC) using a Shimadzu RID-10A (Kyoto, JP), with refractive index detection, Rezex ROA column from Phenomenex (California, USA), isocratic liquid phase consisting of 0.0025 M sulfuric acid with a flow of 0.5 mL min^{-1}. Soluble solids (SS) of fruits were analyzed using a digital refractometer. Parameters of productivity such as fruit numbers, weight (FW), and fruit yield (FY) also were determined.

Three different types of enrichment were performed in two different weeks to analyze the photoassimilates translocation: Two weeks before harvest and at harvest week. The stems containing only one fruit and similar morphological characteristics (stem length and leaf numbers) were identified, and then the leaves were referenced in the primary and secondary stem according to the region in which they werelocated: basal, middle, or apical. Plant growth was observed during the weeks of isotopic enrichment. It was observed that each plant emitted three primary stems, each primary stem emitted secondary stems and the fruit was always on the same node of the first leaf of the secondary older stem, near the primary stem base.

The primary stem and the older secondary stem, which generated the fruit, were divided into three regions of equal size: basal, middle, and apical. Isotopic enrichment was performed on: a) a leaf of the basal region of the primary stem, b) a leaf of the apical region of the primary stem and c) a leaf of the apical region of the secondary stem. For each enriched leaf we collected a group of three leaves from specific regions and the fruit to determine whether these parts received the assimilated ^{13}C. The enriched leaf was also analyzed to establish ^{13}C fixation.

When the enriched leaf was from the basal region of the primary stem (Fig. 1A**, B**), we collected three leaves (in yellow) of the basal, middle, and apical regions of the primary stem; three leaves of the apical region of the secondary stem, the fruit (in brown) and the enriched leaf (in red) to evaluate their isotopic values. When the enriched leaf was from the apical region of the primary stem (Fig. 1C**, D**), we collected three leaves from the basal, middle, and apical regions of the primary stem, the fruit, and the enriched leaf to evaluate their isotopic values. When the enriched leaf was from the apical region of the secondary stem (Fig. 1E**, F**), we collected three leaves from the basal, middle and apical regions of the secondary stem, three leaves from the basal region of the primary stem, the fruit, and the enriched leaf to evaluate their isotopic values.

2.4. Enrichment technique with ^{13}C

The isotopic enrichment using $^{13}CO_2$ gas, from Cambridge Isotope Laboratories Inc. (Massachusetts, USA), was performed by gas transfer from the tank to an acrylic chamber (25 × 30 × 5 cm) with a syringe, allowing an enriched atmosphere for the target leaf. The leaves selected to be enriched were inserted in the chamber, then 8 mL of $^{13}CO_2$ gas with a concentration of 99 % ^{13}C atoms was injected. The injection of $^{13}CO_2$ gas was performed with a gas syringe attached to the cylinder pressure and flow regulator. The syringe was then inserted into the chamber through an orifice sealed with a silicone septum.

The leaves were inserted in the acrylic chamber described above between the hours of 8:00 a.m. and 12:00 p.m., corresponding to the time of high photosynthetic efficiency. Beyond this time solar global radiation rates increase chamber temperature and inhibit CO_2 assimilation. After 30 min of enrichment, the chamber was removed. Samples were collected 6 h after the enrichment period, between 2:30 p.m. and 6:00 p.m. on the same day that $^{13}CO_2$ enrichment was performed. At the time of collection, different organs (leaves and fruits) were identified according to their pertinent region on the stem and immediately immersed in liquid nitrogen (-196 °C) to cause tissue death and avoid any risk of ^{13}C changes. After freezing, samples were stored in an ultra-low temperature freezer (-80 °C) until lyophilization; samples were then

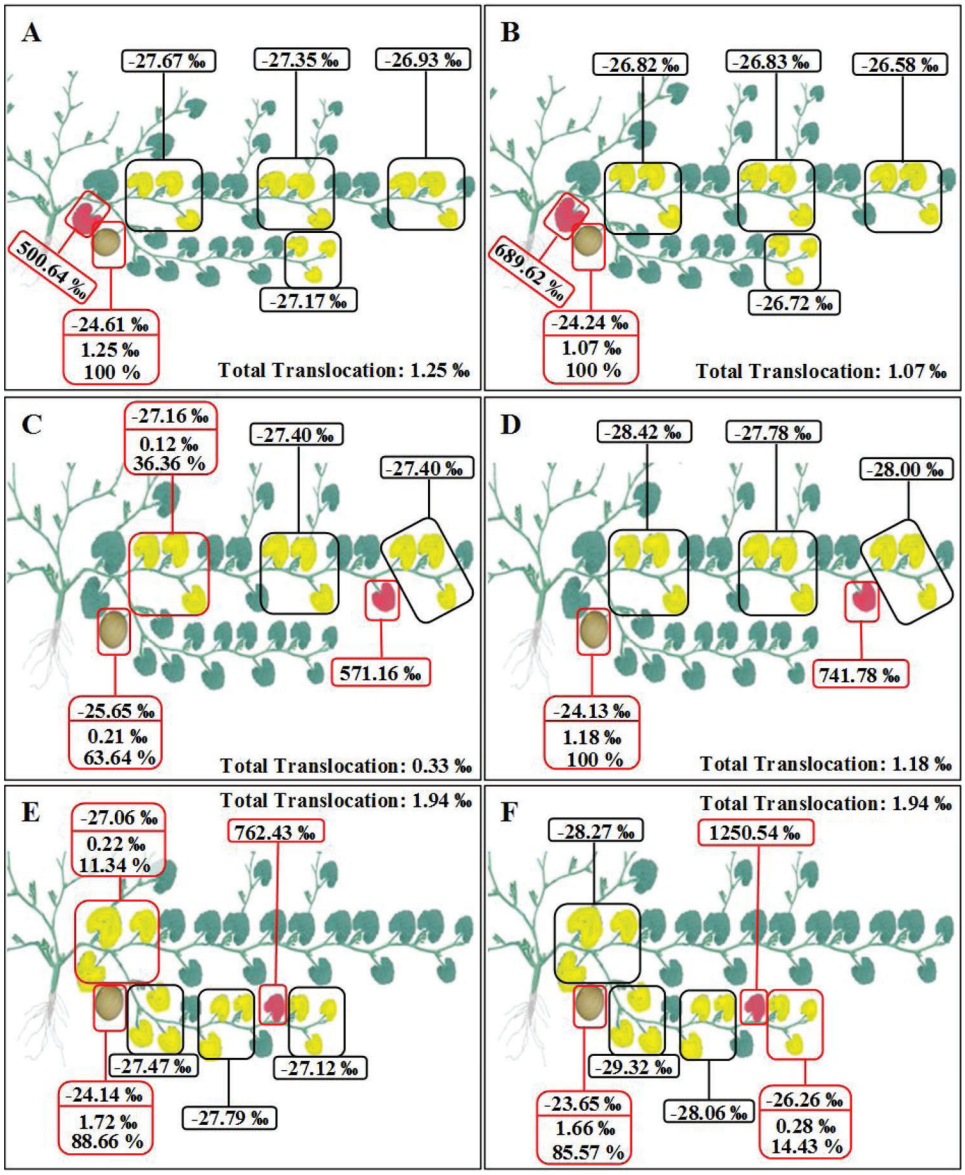

Fig. 1. Leaf enrichment with $^{13}CO_2$ gas two weeks before harvest. Enrichment of the basal leaf of the primary stem in plants irrigated with low-salinity water (A) and with saline water (B). Enrichment of the apical leaf of the primary stem in plants under low salinity (C) and under saline irrigation (D) and enrichment of the apical leaf of the secondary stem in plants under low salinity (E) and under saline irrigation (F). Enriched leaves are depicted in red, analyzed leaves in yellow, and fruits as brown circles. Squares around leaves and fruits mean that the organ received (red) or not (black), ^{13}C from the enriched leaf. Red squares linked to leaves or fruits display absolute (‰) and relative (%) values of translocated ^{13}C from the enriched leaf. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

ground with a mortar and pestle and sieved to obtain a granulometry of <250 μm. Finely ground material is important for sample homogenization, due to the sensitivity and precision of the isotopic ratio mass spectrometer (IRMS), and to minimize differences among sample replicates. Sample preparation steps were carried out in the labs at Embrapa Agroindústria Tropical.

2.5. Isotopic analysis

The ^{13}C analyses of plant samples were carried out at the United States Salinity Laboratory (USDA-ARS) in Riverside, California. A subsample of approximately 500 μg of ground and homogenized material was packed in tin capsules. Tin capsules with samples were inserted into an Elemental Analyzer model Vario Pyro Cube from Elementar (Mt. Laurel, NJ), for the combustion and release of CO_2. The gases generated in the Elemental Analyzer flowed to an Isotopic Ratio Mass Spectrometer, IsoPrime100 from Elementar (Mt. Laurel, NJ). The $^{13}C/^{12}C$ ratio was determined and expressed in δ‰ (delta per thousand), relative notation to VPDB standard as described by (Sulzman, 2007). The results were obtained from a calibration curve using known δ ^{13}C standards (EDTA, USGS40, and Sodium Bicarbonate - IAEA 303).

The ^{13}C translocation was analyzed by measuring the natural value in leaves of each region (basal, middle, and apical) of the stem and the fruit. These analyses were made to determine the value of $\delta^{13}C$ that occurs under natural environmental conditions of our experiment for the melon crop. In this way, it is possible to compare the results obtained before and after leaf enrichment with $^{13}CO_2$ to establish whether there was ^{13}C fixation during enrichment.

The $\delta^{13}C$ natural values of leaves and fruits were submitted to analysis of variance and comparison of means to obtain differentiation information among plant regions in the treatments or between treatments. From the average of three replicates, a starting point (SP) of $\delta^{13}C$ was considered and an isotope scale was constructed considering this limit as a standard (Fig. 2). Thus, any sample that had a $\delta^{13}C$ value less negative than the starting point was enriched in ^{13}C relative to the standard.

2.6. Statistical analyses

The analysis of variance was performed in a factorial system for Na, Cl, sucrose, CO_2 assimilation rate, and $\delta^{13}C$ natural in leaves and fruit, considering salinity (ECw) as the main factor and stem region as the

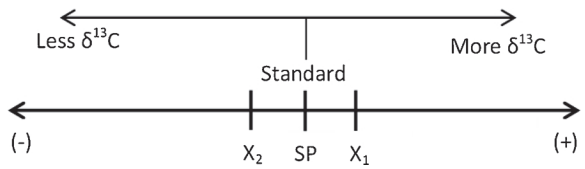

Fig. 2. Isotopic scale showing enrichment directions of $\delta^{13}C$ related to the Start Point (SP), where X_1 represents a sample richer in ^{13}C and X_2 represents a sample richer in ^{12}C.

secondary factor (ECw x Stem Region). Another analysis of variance was performed in a factorial system for the parameters fruit weight, soluble solids, and fruit sucrose, considering salinity (ECw) as the main factor and collection week (two weeks before harvest and at harvest week) as the secondary factor (ECw x Week). For fruit yield, only the salinity factor was analyzed at harvest week. Tukey's test at the 5 % level of significance was used to compare means. Statistical analyzes were performed using statistical software Sisvar® (Ferreira, 2000). The descriptive analysis of $\delta^{13}C$ data was adopted to characterize the translocation of photoassimilates.

3. Results

3.1. Leaf parameters

At two weeks before harvest, the CO_2 assimilation rate was similar for all treatments and its mean value was 15.7 μmol m^{-2} s^{-1}, regardless of salinity or stems region (Fig. 3A). Two weeks before harvest, sucrose, Na and Cl concentration had a significant interaction between factors ECw and Stem Region (Fig. 3B**, C, D**).

Leaf sucrose concentration in plants under salinity was greater than in control plants, for all stem regions analyzed, and plants under salinity had 28.1 % more sucrose in apical leaves of secondary stem than in basal leaves of primary stems (Fig. 3B). In control plants, there was no significant difference in sucrose concentration between leaves from apical and basal positions (Fig. 3B).

Two weeks before harvest, leaf Na and Cl concentrations were higher in the basal leaves of plants under saline stress than any other region. Plants irrigated with saline water had more leaf Na and Cl than did the control plants, regardless of the stem region. The Na concentration in leaves of plants under salinity were 50.5 % to 145.9 % greater in relation to the control plants (Fig. 3C), whereas for Cl this variation was 32.2 % to 103.2 % (Fig. 3D).

In control plants, Na (5.3 mg g^{-1} DM) and Cl (21.1 mg g^{-1} DM) concentrations remained constant among the different stem regions. In plants under saline stress, Na and Cl concentrations decreased from basal to apical region of both primary and secondary stems. Comparing control plants with those under salinity, Na concentration of basal leaves of primary stem in plants under salinity increased by 145.9 %, while in the apical region of the same stem Na concentration increased by 82.1 %. A similar, and significant, difference was observed between the basal and apical leaves in secondary stems (Fig. 3C). Basal leaves of the primary stem had Cl concentrations of 39.1 mg g^{-1} DM for plants under salinity and 19.3 mg g^{-1} DM for control plants, while apical leaves had 32.2 and 18.8 mg g^{-1} DM for saline vs. low-salinity (Fig. 3D).

At the week of fruit harvesting, both CO_2 assimilation rate and sucrose had significant differences in response to salinity and stem region when analyzed in isolation, but the interaction of these factors was not significant (Fig. 4A**, B**). The concentrations of Na and Cl had significant interaction for ECw and Stem Region factors at harvest week (Fig. 4C**, D**).

At fruit harvest week, control plants photosynthesized more than plants under salinity. Regarding the stem region, apical leaves of primary and secondary stems assimilated more CO_2 than basal leaves of stems, independent of salinity (Fig. 4A). While the average of CO_2 assimilation rate two weeks before harvest was 15.7 μmol m^{-2} s^{-1}, during fruit harvest week basal leaves of primary and secondary stems had average CO_2 assimilation rates of 8.97 and 8.14 μmol m^{-2} s^{-1}, respectively (Fig. 4A). Apical leaves had CO_2 assimilation rates of 12.6 and 13.2 μmol m^{-2} s^{-1} for primary and secondary stems respectively, differing statistically from basal leaves (Fig. 4A).

Among the leaf sugars analyzed, sucrose concentration was greater in plants under salinity (+28.9 %) than in control plants. Although sucrose concentration between leaves of different stem regions was different, apical leaves of secondary stems and basal leaves of the primary stem did not differ significantly in sucrose concentration, independently of ECw (Fig. 4B).

The highest Na and Cl concentrations, at harvest week, were recorded in all regions of primary stem and the basal region of the secondary

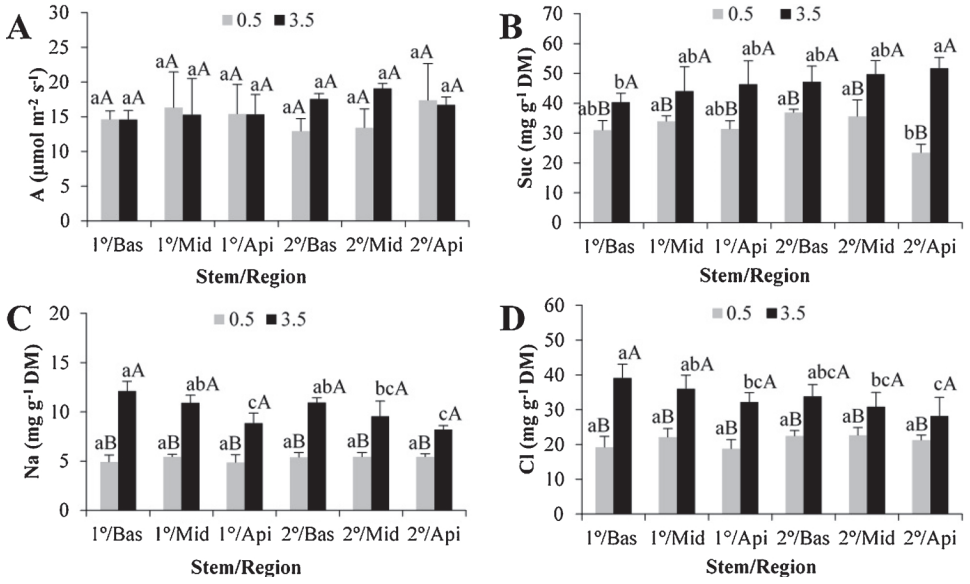

Fig. 3. Leaf physiological parameters of melon plants two weeks before harvest. CO_2 assimilation rate - A (A), sucrose - Suc (B), sodium - Na (C), and chloride - Cl (D). Values followed by different uppercase letters are significantly different at $P < 0.05$ regarding irrigation-water salinity, while values followed by different lowercase letters are significantly different at $P < 0.05$ for different stem regions. Stem type: 1° - primary, 2° - secondary. Regions: Bas – basal, Mid – middle, Api – apical.

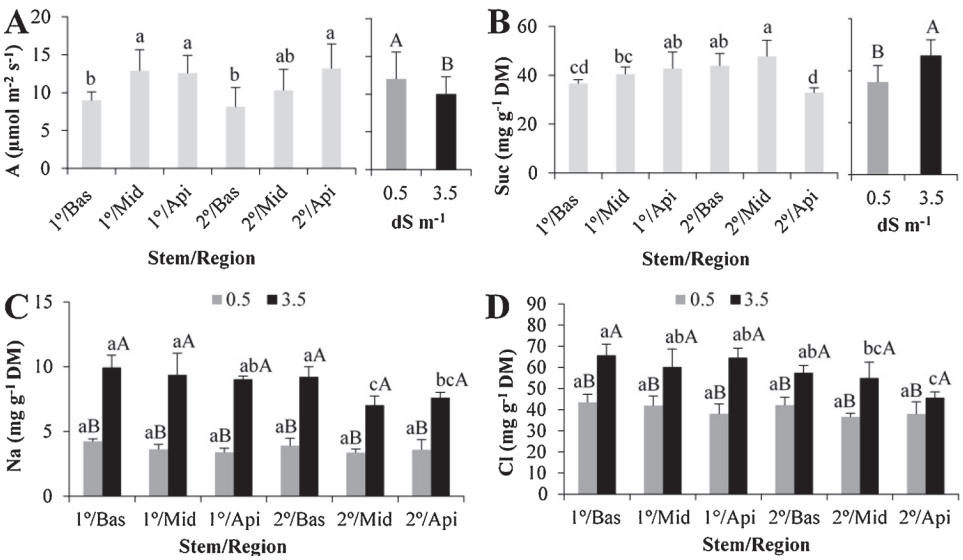

Fig. 4. Leaf physiological parameters of melon plants during harvest week. CO_2 assimilation rate - A (A), sucrose – Suc (B), sodium – Na (C), and chloride – Cl (D). Values followed by different uppercase letters are significantly different at $P < 0.05$ regarding salinity, while values followed by different lowercase letters are significantly different at $P < 0.05$ for different stem regions. Stem type: 1° - primary, 2° - secondary. Regions: Bas – basal, Mid – middle, Api – apical.

stems. Sodium concentration in leaves of plants under saline stress increased over 100 % in comparison to control plants for all analyzed regions (Fig. 4C). Chloride concentration in leaves was up to 70 % higher in plants irrigated with saline water relative to control treatment (Fig. 4D).

3.2. ^{13}C in melon plants

A significant differentiation of $\delta^{13}C$ natural isotopic value was observed between different plant parts in control plants (0.5 dS m^{-1}). In plants exposed to salinity (3.5 dS m^{-1}), significant differences were only found for $\delta^{13}C$ natural values between leaves and fruits, but not for leaf age (Fig. 5).

The $\delta^{13}C$ natural isotopic values of leaves in plants under salinity was -26.54‰, regardless of the stem region analyzed, and the $\delta^{13}C$ natural value in fruits was -25.31‰. For the control treatment, the much younger leaves had more $\delta^{13}C$ natural values. For basal, middle, apical leaves and for fruits $\delta^{13}C$ natural values were -27.28, -27.00, -26.54, and -25.81‰, respectively (Fig. 5).

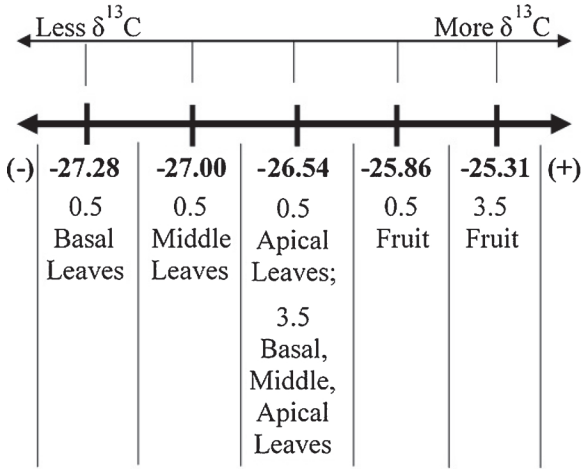

Fig. 5. Natural $\delta^{13}C$ (‰) in different parts of the plant. ECw: 0.5 and 3.5 dS m^{-1}. Stem regions: basal, middle, apical leaves, and fruit. Parts that had less negative values than the values listed on the above scale indicate that they received ^{13}C from the enriched leaf.

The $\delta^{13}C$ natural isotopic values were standardized to evaluate, in leaves and fruits, whether photoassimilates were received from the leaf enriched with the $^{13}CO_2$ gas. The less negative $\delta^{13}C$ value in comparison to the standard value (Fig. 5) means that the organ (leaf or fruit) received more translocated ^{13}C.

Enriching the basal leaf of the primary stem two weeks before harvest resulted in 100 % of the ^{13}C translocated by the enriched leaf being directed to the fruit, regardless of whether plants were irrigated with saline water or control (low salinity) water (Fig. 1**A, B**). The ^{13}C total translocation from enriched leaf in control plants was 1.25‰ (Fig. 1A) and under saline stress was 1.07‰ (Fig. 1B).

When enriching the apical leaf of the primary stem of plants irrigated with saline water it was noticed that 100 % of the ^{13}C translocated also went into the fruit, translocating an absolute value of 1.18‰ (Fig. 1D). In contrast, the ^{13}C total translocation in control plants was only 0.33‰ (Fig. 1C), directing 63.64 % for the fruit and 36.36 % for basal leaves of the primary stem.

The isotopic enrichment of the apical leaf of the secondary stem showed that the ^{13}C translocated was the same for plants grown with saline (Fig. 1F) and low-salinity water (Fig. 1E), with an absolute value of 1.94‰. However, the distribution of this value occurred differently between plants irrigated with saline and low-salinity water. In control plants, the translocation occurred for the fruit and for basal leaves of the primary stem (Fig. 1E), while in plants under salinity the translocation occurred for fruits and leaves near the enriched leaf, in the apical region of secondary stems (Fig. 1F). The percentage directed from apical leaves of the secondary stem to fruit was 88.66 % and 85.57 % for control plants and plants under salinity, respectively. Plants under salinity invested the ^{13}C remaining (14.43 %) in the adjacent leaves (Fig. 1F) while control plants exported 11.34 % of ^{13}C to basal leaves of the primary stem (Fig. 1E). It is important to note that the absolute value exported by the enriched apical leaf of the secondary stem was approximately double the value translocated by the enriched basal leaf of the primary stem.

The pattern of translocation for photoassimilates during harvest week changed compared to two weeks before harvest. Analyzing the translocation from the enriched basal leaf of the primary stem of control plants from two weeks before harvest to harvest week, there was a reduction of the absolute value translocated from 1.25 to 0.71‰ (Fig. 1**A;** Fig. 6A). In contrast, in plants under salinity, the value doubled from 1.07 to 2.16‰ (Fig. 1**B;** Fig. 6B). Leaves of basal region in plants

under salinity translocated three times more ^{13}C (2.16‰) than basal leaves in control plants (0.71‰) (Fig. 6A, B).

While two weeks before harvest basal leaves of primary stems translocated all ^{13}C to the fruit (Fig. 1A, B), during harvest week there was a differentiation in the partitioning and the percentage of distribution between plants cultivated with saline and low-salinity water (Fig. 6A, B). The ^{13}C percentage directed from enriched leaf to the fruit in control plants was only 4.23 %, representing a ^{13}C absolute value of 0.03‰. The ^{13}C remaining was translocated to leaves of the same region (60.56 %) and to middle leaves of the same stem (35.21 %), (Fig. 6A). The fruit, in plants under salinity, continued to receive a ^{13}C absolute value close to 1‰, which in terms of percentage was 42.60 %. The remaining ^{13}C was translocated to leaves of the same region and middle region of the same stem, in the salinity and control, and to apical leaves of the secondary stem (0.05‰) (Fig. 6B).

When the apical leaf of the primary stem was enriched in the harvest week, absolute values translocated (0.42‰ in control plants and 1.02‰ in plants under saline stress) approached those determined when the enrichment was done two weeks before harvest (0.33 and 1.18‰, to control plants and saline treatment, respectively), but with a different distribution pattern of the ^{13}C. Apical leaves of the primary stem in control plants did not export ^{13}C to the fruit. The translocation was only for basal leaves (52.38 %) and for middle leaves of the same stem (47.62 %) (Fig. 6C). When analyzing plants irrigated with saline water, it was observed that the enriched leaf still contributed ^{13}C to the fruit, with a total translocated value of 53.92 % or 0.55‰ of the ^{13}C absolute value (Fig. 6D), approximately half of the quantity translocated two weeks before harvest (1.18‰). The other 0.47‰ of ^{13}C translocated by the enriched leaf in this region was similarly distributed among the other evaluated parts (Fig. 6D).

The enrichment of the apical leaf of the secondary stem indicates that this leaf at the end of the cycle reduced the volume of ^{13}C translocated regardless of whether or not plants were irrigated with saline water. The reduction was greater in control plants (reduction of the ^{13}C absolute value was from 1.94 to 0.30‰) (Fig. 1E; Fig. 6E), while in plants irrigated with saline water the decrease was from 1.94 to 0.69‰ (Fig. 1F; Fig. 6F). For the total ^{13}C translocated from apical leaves of the secondary stem in control plants, only 0.04‰ was destined to the fruit, which represents 13.33 %. Also, the region that received the most ^{13}C was the basal region of the primary stem, 63.34 % of the total translocated (0.19‰). For the other evaluated parts, only the apical region of the primary stem did not receive ^{13}C fixed by the enriched leaf (Fig. 6E).

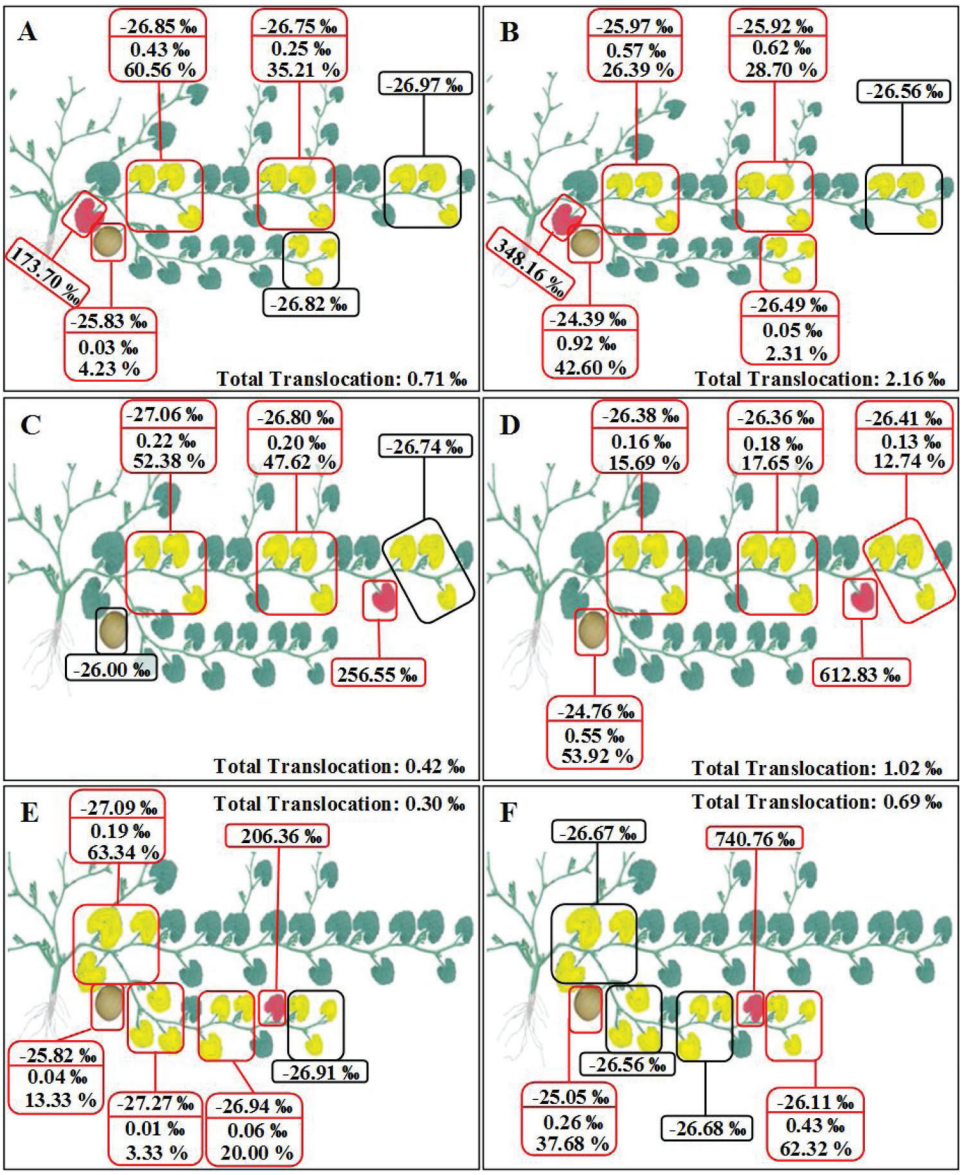

Fig. 6. Leaf enrichment with $^{13}CO_2$ gas in the harvest week. Enrichment of the basal leaf of the primary stem in plants irrigated with low-salinity water (A) and with saline water (B). Enrichment of the apical leaf of the primary stem in plants under low-salinity irrigation (C) and under saline irrigation (D) and enrichment of the apical leaf of the secondary stem in plants under low-salinity (E) and under saline irrigation (F). Squares around leaves and fruits mean that the organ received (red) or not (black), ^{13}C from the enriched leaf. Red squares linked to leaves or fruits display absolute (‰) and relative (%) values of translocated ^{13}C from enriched leaf. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

In plants under salinity, the ^{13}C distribution continued to occur to the fruit and to apical leaves. The percentage directed to the fruit in the harvest week was 37.68 % (0.26‰) and for the adjacent leaves was 62.32 % (Fig. 6F).

In control plants, the basal leaves of the primary stem and apical leaves of the secondary stem are the main carriers of carbohydrates to the fruits two weeks before harvest. The three enriched leaves (basal and apical of the primary stem, and apical of secondary stem) in the saline condition contributed carbohydrate to fruits.

Enriched leaves from control plants in the harvest week contributed little or no ^{13}C to fruit. In contrast, in plants under salinity, enriched leaves of all three regions continued carrying ^{13}C to the fruit, although only basal leaves of the primary stem continued to export in great quantity, whereas apical leaves of primary and secondary stems decreased the export to fruit when compared to two weeks before harvest.

3.3. Fruit parameters

Both fruit number (Fig. 7) and fruit yield (Fig. 8B) were analyzed only during harvest week, showing a significant difference in response to salinity. The analysis of the other fruit parameters: weight, sucrose, and soluble solids established a significant interaction between the factors ECw and Week (Fig. 8A**, C, D**).

Plants irrigated with saline water had significantly less (Fig. 7) and lighter (Fig. 8A) fruits than plants irrigated with low-salinity water. Plants irrigated with saline water had significantly fewer fruits (2 fruits each) compared to plants irrigated with control water (3 fruits each) (Fig. 7). While fruits of control plants increased 303 g between the evaluated weeks, fruits of plants under salinity increased 245 g. Fruits of plants under salinity, two weeks before harvest, were approximately 35.9 % lighter when compared to fruits of control plants (Fig. 8A). The weight difference in the salinity vs. control was 30.9 % in harvest week (Fig. 8A).

The final yield of the 'Zielo' hybrid was 18.90 T ha^{-1} for plants irrigated with low-salinity water, while for plants irrigated with saline water the yield was 8.71 T ha^{-1} (-53.9 %) (Fig. 8B).

Among the sugars analyzed, sucrose was significantly higher in fruit harvest week when it was compared with two weeks harvest regardless of salinity (Fig. 8C). Sucrose values two weeks before harvest did not differ significantly between saline and low-salinity treatments, with values of 0.87 and 1.17 mg mL^{-1} Pulp. Control plants in the fruit harvest week had a sucrose concentration significantly higher than plants under salinity, with values of 97.14 and 84.52 mg mL^{-1} Pulp, respectively (Fig. 8C).

There was no significant difference in soluble solids of fruits of plants under saline and low-salinity, treatment regardless of the week evaluated. At two weeks before harvest, soluble solids of fruits of control (low-salinity water) plants and under salinity were respectively 6.4 and 6.3°Brix, while at the end of the cycle fruits °Brix increased to 13.3 and 14.4 in control plants and under salinity, respectively (Fig. 8D).

4. Discussion

Regarding Na and Cl leaf concentration, the differential accumulation observed between old and young leaves (Fig. 3C**, D;** Fig. 4C**, D**) was probably due to differential effects of evapotranspiration and salinity to these leaves. Older leaves probably received more total water and salts than young leaves due to the longer exposure of older leaves to saline water. In addition, plants may have adopted a strategy of maintaining low Na and Cl concentrations in younger leaves to reduce salt deleterious effects on photosynthesis and other physiological or biological functions. Kuşvuran (2012) evaluated Na concentration in young and mature leaves of melon during their initial development and observed that increased irrigation water salinity led to a higher accumulation of salts in older than in younger leaves.

In our study, leaf salt (Na and Cl) concentrations increased due to salinity increase in the irrigation water. Chloride, but not Na, concentration continued to increase during the two final weeks of fruit development, including the harvest week. Chloride concentrations may have increased progressively as plants got older. The same does not always happen for Na concentration indicating that Na uptake can be partially controlled at the root (Dias et al., 2016; Lima et al., 2020; Prior et al., 2007; Sarabi et. al., 2017). In general, plants do not have a control mechanism for Cl absorption, although they can control Na (Dias et al., 2016). Confirming our results for Na and Cl leaf concentration, Tedeschi et al. (2017) and Lima et al. (2020) observed an increase in the concentration of these ions in leaves when salinity of irrigation water increased.

Plants under saline stress had lower CO_2 assimilation rates than control plants at the harvest week (Fig. 4A), and this fact may be associated with toxic effects of absorbed salts (Na and Cl) and the partial closure of stomata due to a reduction in stomatal conductance. Stomatal conductance and CO_2 assimilation are strongly correlated and often decline to a similar extent in plants exposed to environmental stress (Wong et al., 1985). While a reduction in stomatal conductance will restrict the entry of CO_2 into a leaf, the photosynthetic capacity of the mesophyll may decline in response to the same factors that cause stomatal closure. Often the initial effect of drought or increased salinity is a reduction in the apparent ribulose-1.5-bisphosphate (RuBP)-regeneration capacity (estimated from the photosynthetic at high CO_2) (Farquhar et al., 1987). In agreement with this study, Colla et al., 2006, studying watermelon, Lima et al. (2020) and Roupahel et al. (2012), studying

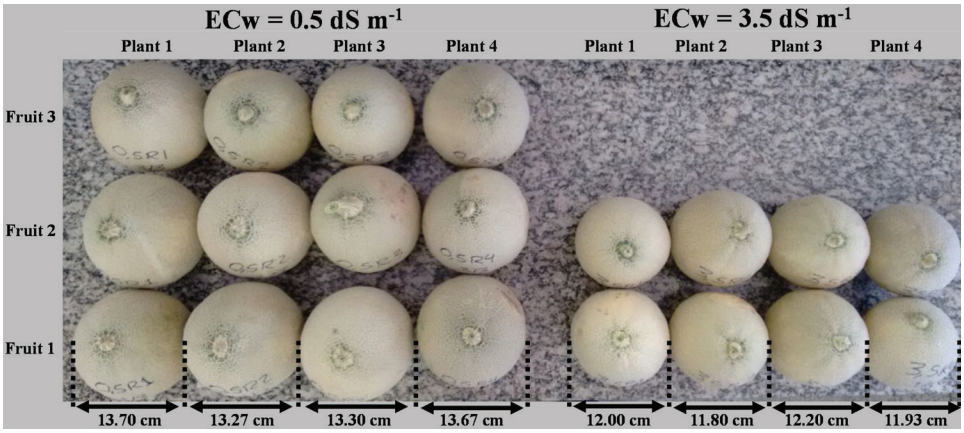

Fig. 7. Difference between fruit sizes obtained from plants irrigated with low-salinity water (left) or with saline water (right) during harvest week. Equatorial fruit diameter fruit (EFD) is shown at the figure base. Average EFD for low-salinity condition was 13.49 cm and 11.98 cm for saline condition.

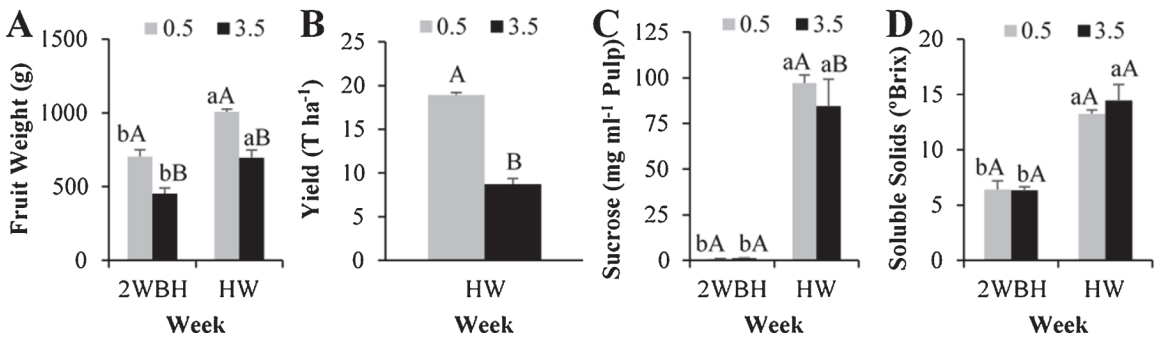

Fig. 8. Fruit parameters. Fruit weight (A), yield (B), sucrose (C), and soluble solids (D). Week: 2WBH- Two weeks before harvest, HW- Harvest week, ECw: 0.5 and 3.5 dS m^{-1}. Values followed by different uppercase letters are significantly different at $P < 0.05$ regarding salinity factor and values followed by different lowercase letters are significantly different at $P < 0.05$ regarding week factor.

melon plants, observed a decrease in CO_2 assimilation rate with increased salinity. The fact that older leaves of control plants had a decreasing CO_2 assimilation rate from two weeks before harvest to harvest week indicates that senescence and the onset of leaf abscission, both controlled by abscisic acid (Song et al., 2016), affect stomatal opening, supporting the findings of reduced translocation of photoassimilates to the fruit (Fig. 6A).

The highest sucrose concentrations found in leaves of plants under saline stress (Fig. 3**B;** Fig. 4B) could be attributed to osmotic adjustment. Under osmotic stress, plants can accumulate osmotically-compatible solutes to lower osmotic potential, and maintain cell turgor and physiological processes (Turner, 2017). In plants, there are two kinds of osmolytes mediating osmotic adjustment, organic solutes, such as sucrose, polyols, glycine betaine, and proline; and inorganic ions, such as K^+, Ca^{2+}, Na^+, Mg^{2+}, and Cl^- (Chen and Jiang, 2010). This increase in sucrose concentration in stressed leaves may also be due to a reduction in the translocation of photoassimilates as a function of the smaller concentration of sucrose in other sinks, which is evidenced by the reduction in the growth of those plants. Similar increases in cell sugar concentration in response to stress were observed by Sarabi et al. (2017); Purinan-Harley et al. (2014), and Zhu (2001).

Plants of C3 metabolism, such as melon, have a greater preference for the fixation of ^{12}C by the enzyme RUBISCO, and this fact leads to a higher ^{13}C discrimination of C3 plants as compared to C4 plants, for example. Previous studies have observed less ^{13}C discrimination when plants were submitted to salinity (Bagues et al., 2018; Borzouei et al., 2020; Eskandari et al., 2012; Groenigen and Kessel, 2002; Poss et al., 2000; Shaheen and Hood-Nowotny, 2005; Sarabi et al., 2017). The ^{13}C natural values in plants under salinity were higher than in control plants (Fig. 5) because plants under stress discriminate less between ^{12}C and ^{13}C. This discrimination is probably due to a decrease in the selectivity of RUBISCO by ^{12}C (Kellogg, 2013), producing more ^{13}C photoassimilates in their composition or to both diffusion limitations associated with reduced stomatal conductance and reductions in photosynthetic efficiency related to decreases in ribulose-1.5-bisphosphate (RuBP) carboxylase activity (Bagues et al., 2018). Some authors also attribute the low RUBISCO discrimination by ^{13}C in saline conditions to stomata partial closure, which causes a lower $^{12}CO_2$ partial pressure, thus leading to a higher $^{13}CO_2$ assimilation (Guy et al., 1980; Walker and Sinclair, 1992).

For the control treatment, the much younger apical leaves had higher ^{13}C natural values expressed by the lower negative value of -26.54‰ (Fig. 5). This may be associated with the rapid growth of apical leaves due to the high expansion and cell division, leading to a high requirement of photoassimilates. Silva et al. (2011), studying the natural variation of ^{13}C in fig plants, found that the new parts of the stems showed average isotopic values of -28.41‰; -28.43‰ and -28.51‰, indicating higher values of ^{13}C in the newly opened leaves, apical bud and fruits, respectively, to the detriment of other parts of the stem. Cernusak et al. (2009), evaluating *Ficus insipida* plants growing in the forests of Panama found $\delta^{13}C$ values that ranged from -29 to -27‰ in the leaves.

At two weeks before harvest, there was no preferential source for fruit formation both in control and in stressed plants (Fig. 1), with both basal and apical leaves exporting the same carbohydrate quantities to fruits. The lack of differentiation between treatments shows that fruits are the major sink two weeks before harvest, requiring most of the photoassimilates. This demand is associated with the beginning of fruit maturation.

The differentiation of ^{13}C translocation between organs of plants irrigated with saline water and the low-salinity-water control in the harvest week (Fig. 6) shows that control plants probably completed the fruit filling prior to harvest week, while plants under salinity continued to incorporate ^{13}C into the fruit, this is corroborated by the lower fruit weight in plants under salinity. For plants under saline stress, fruits remain as the main photoassimilate sink, suggesting that stressed plants had a delay in their natural development mediated by the translocation delay of photoassimilates from leaves. This phenomenon is linked to the energy expenditure of these plants as they try to compensate for the deleterious effects of salinity, such as the energy spent to block Na absorption and to regulate cellular osmotic adjustment, all of which inhibit the transfer of photoassimilates to the fruit.

Melon producers generally cease fertigation two weeks before harvest to reduce fertilizer costs, believing that the possible gain in fruit size and quality is not cost-effective. It should be noted that stopping fertigation two weeks before melon harvest, as is adopted by producers irrigating with low-salinity water, can disturb the transport of photoassimilates under stress (salinity) conditions. This is suggested by our results, in that plants irrigated with saline water during harvest week had delayed translocation of carbohydrates from leaves to the fruits, a process that may still require minerals provided during fertigation.

The results of our study confirm those reported by Bagues et al. (2018) and Borzouei et al. (2020). Both studies reported that both barley and wheat plants discriminated less ^{13}C when irrigated with saline waters. We have previously discussed why there was less discrimination between ^{12}C and ^{13}C under saline conditions.

Results for carbohydrate translocation were also reported by Finazzo et al. (1994) and Vasconcelos (2001) when studying avocado and passion fruit crops under salinity. Our results with melon (Fig. 1) agree with the results of both reports during the reproductive phase of both crops in that the photoassimilates produced by the enriched leaf were almost entirely imported by fruits, which are major sinks during the reproductive phase.

Our results on carbohydrate translocation in melon plants irrigated with low-salinity water, regardless of the week evaluated (Figs. 1A, 6 A), also agree with those of Lai et al. (1988) working with kiwi, who reported that not all leaves above the enriched leaf received photoassimilates from that leaf. During the two weeks before the end of the

experiment, there was no carbohydrate translocation from the enriched leaf at the base of the stem to any younger leaf towards the stem tip because all photoassimilates were translocated to the fruit (Fig. 1A), the major sink at the final development stage. During the last week, with fruits completely developed in control plants, there was some carbohydrate translocation from basal leaf to younger leaves, but not to the youngest leaves at the tip (Fig. 6A).

Opposite than what was reported by Kriedemann (1969) in lemon tree leaves, melon leaves in our experiment did not have to mature completely to transfer carbohydrates. Enriched leaves from the top of branches transferred photoassimilates not only to the fruit (Fig. 1C), but also to other leaves in the same branch (Fig. 6C). Young melon plant leaves transferred carbohydrates the same (or more) than mature leaves as they had similar photosynthetic activity to mature leaves (Fig. 3A, 4 A). Another thing to consider is that melon plant leaves have a short cycle and an intense metabolic rate leading them to start transferring carbohydrates earlier.

The lower fruit weight, and consequently the lower yield of plants irrigated with saline water (Fig. 8A**, B**) may be associated with the delay in fruit cycle mediated by the restriction of photoassimilate translocation to fruits during maturation. Reduction in fruit weight was also reported by Del Amor et al. (1999) and Tedeschi et al. (2011) when ECw was increased. Several authors reported fruit yield decreases with salinity: Freitas et al. (2014) reported a decrease of 11 % in 'Orange Flesh' melon, Melo et al. (2011) of 16 % in 'Galia' melon, and Lima et al. (2020) of 12.4 % in 'Cataloupe' melon, for each unit increased in ECw. Huang et al. (2012) observed that the cultivar tolerance was only up to 2.7 dS m^{-1}, after which there was a 12.7 % decrease of yield per unit increase in soil EC of the saturation extract (ECe). Tedeschi et al. (2011) also reported that melon plants cultivated in the Mediterranean region tolerated salinity up to ECe of 1.73 dS m^{-1}, and that, after this value, there was a 12 % decrease in yield per each unit of increased ECe.

5. Conclusions

An increase in irrigation water salinity from 0.5 to 3.5 dS m^{-1} delayed the photoassimilate flow between source and sink. Increasing Na and Cl concentrations in irrigation water during plant development decreased vegetative and reproductive development.

Leaves of plants irrigated with low-salinity water considerably reduced the photoassimilate contribution to the fruit, completing fruit maturation during harvest week, while leaves of plants irrigated with saline waters continued to contribute with a high precentage of photoassimilates to fruits.

An increase in irrigation water salinity from 0.5 to 3.5 dS m^{-1} resulted in a decrease of 53.9 % in fruit yield, not only due to reduced fruit size, partly mediated by the delay in carbohydrate translocation, but also due to the significant and consistent reduction of one fruit per plant. Results suggest that fertigation can be stopped in the last week from harvest when using low-salinity water, consistent with melon producers' current practices. However, this practice is not beneficial in conditions of salt stress, as carbohydrate transport continues, with consequent demand for nutrients. Further studies are needed to determine if extending the crop cycle under salinity may compensate for delayed fruit maturation and, maybe, increase fruit sugars.

CRediT authorship contribution statement

Reivany E.M. Lima: Conceptualization, Methodology, Data curation, Formal analysis, Writing - review & editing. **Luciana F. de L. Farias:** Formal analysis, Methodology. **Jorge F.S. Ferreira:** Formal analysis, Supervision, Writing - review & editing. **Donald L. Suarez:** Formal analysis, Supervision, Writing - review & editing. **Marlos A. Bezerra:** Conceptualization, Methodology, Data curation, Formal analysis, Supervision, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at doi:https://doi.org/10.1016/j.scienta.2020.109659.

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