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Research article

Impact of wild solanaceae rootstocks on morphological and physiological response, yield, and fruit quality of tomato (*Solanum lycopersicum* L.) grown under deficit irrigation conditions

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A R T I C L E I N F O

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A B S T R A C T

It has been established that climate change has a direct impact on water availability, an essential resource for agricultural development. As a result, controlling, mitigating, and adapting to water deficit requires the advancement of research on promising wild flora species. As recent studies have shown, wild relatives of certain cultivars are tolerant to adverse factors, enabling the development of sustainable and resilient agriculture. The present study evaluated the morpho-physiology and productivity of tomato scions grafted on wild Solanaceae (*Datura stramonium*, *Solanum sisymbriifolium*, *Solanum quitoense*, and *Cyphomandra betacea*) grown under water deficit conditions (100% ETc - high level, 75% ETc - moderate level, 50% ETc - medium level, and 25% ETc - low level). The results showed that tomato plants grafted on *Datura stramonium* rootstocks performed better morpho-physiologically under deficit irrigation. The improved osmoregulation caused by a higher relative water content (98.49%) allowed the scion to be more tolerant to water stress. In addition, these scions showed high water potential during their phenological stages (vegetative −0.47 MPa, flowering −0.59 MPa, and production −0.64 MPa), as well as improved photosynthetic efficiency. The overall tolerance of the scion resulted in better yield (8.14 kg/plant) with higher number of commercially valuable fruits. The *D. stramonium* rootstock allowed better management and use of irrigation water, increasing productivity (54.95 kg/m^3); that is, it is presented as a species with potential for establishing tomato production areas in scenarios of water scarcity or cultivation under deficit irrigation.

1. Introduction

Tomato (*Solanum lycopersicum* L.) is one of the most important vegetables in the world, with an estimated production of 186 million tons per year [1]. However, problems with stressors (caused by climate change), such as persistent droughts, increased salinity, and

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decreased quality and quantity of water resources, can limit the availability of arable land and productivity potential [2–6].

Water availability is a critical resource for the life cycle of plants. In a water deficiency scenario, changes in biochemical, physiological and morphological processes may occur, resulting in a delay in growth and development, decreasing yields [7–9]. In tomato, the imposition of water stress during growth can benefit fruit quality by allowing an increase in total soluble solids levels [10]. However, the tomato plant is particularly sensitive to water deficit during reproductive development, as it causes physiological disturbances leading to the loss of flower buds and open flowers, as well as a reduction in fruit set, which has a negative impact on commercial yield [11]. Therefore, to develop sustainable agriculture that uses less water resources, it is imperative to explore genetic biodiversity as a key factor to improve yield, crop quality and resistance to stress (biotic and abiotic) [12]. Consequently, the FAO's most important proposal is the development of drought-tolerant crops [13], since irrigation systems, as a measure to mitigate the consequences of a water deficit, has its own economic and environmental costs, indicating that this option is not suitable for all scenarios [14]. This proposal calls for the identification and use of species/cultivars best suited to each cropping area to enable farmers to maintain crop productivity even under unfavorable environmental conditions [12].

Numerous wild-type Solanaceae species, such as *S. nigrum*, *S. torvum*, *S. pimpinellifolium*, *S. chilense*, and *S. peruvianum*, have been described to have phenotypic traits that confer abiotic stress tolerance [15–19]. The wild type of *Solanum* includes plants that have evolved root systems that give them a high capacity to absorb water and nutrients from a variety of environmental conditions, ranging from coastal desert climates to wet and foggy conditions [15,17,18]. Due to the various combinations of stressors (drought, salinity, heavy metals, UV radiation, and cold) to which these species are exposed as a result of their diverse geographic distribution and habitat, they have evolved new characteristics that allow them to tolerate stressful conditions [18,19]. Thus, these species may be potential sources of benefits with a view to possible crop improvement.

Grafting is seen as a viable and sustainable alternative to promote tolerance to diseases, abiotic stress factors and/or increase production of vegetables such as cucurbits and Solanaceae [20,21]. More recent studies have indicated that grafting can be a powerful method to promote water stress tolerance in crop shoots [22–24]. For example, the use of 'A25' rootstock, a water scarcity tolerant bell pepper accession, has been shown to alleviate the severity of water stress in 'Adige' bell pepper scions versus ungrafted plants grown under the same conditions [25]. In addition, root growth and vigor, as well as N, P, K, Ca, and Mg concentration of scion grafted on drought-tolerant tomato rootstock ('606', T) was significantly higher compared to those grafted with susceptible seedlings ('112', S) [23]. Grafting has proven to be an effective strategy to improve tolerance to stress factors; therefore, wild Solanaceae, a source of high genetic variability, could be used as rootstock to promote the development of plants resilient to different stress factors [26–28].

Grafting is used to investigate the transmissibility of physiological signals between a lower plant (mother plant) and its associated plant (scion) in response to abiotic and biotic signals [29]. This technique is based on a mechanical injury that causes an accelerated closure of the cut to prevent water loss and the entry of pathogens [30,31]. Therefore, growing grafted plants requires a high degree of skill in tissue manipulation, as well as species compatibility that allows a successful connection between the mother plant and the scion [29]. In addition, it is essential to continue investigating the effect of grafting, as it may have unfavorable results on some aspects of fruit quality, such as dry matter, soluble solids concentration, total sugar and vitamin C content [32,33].

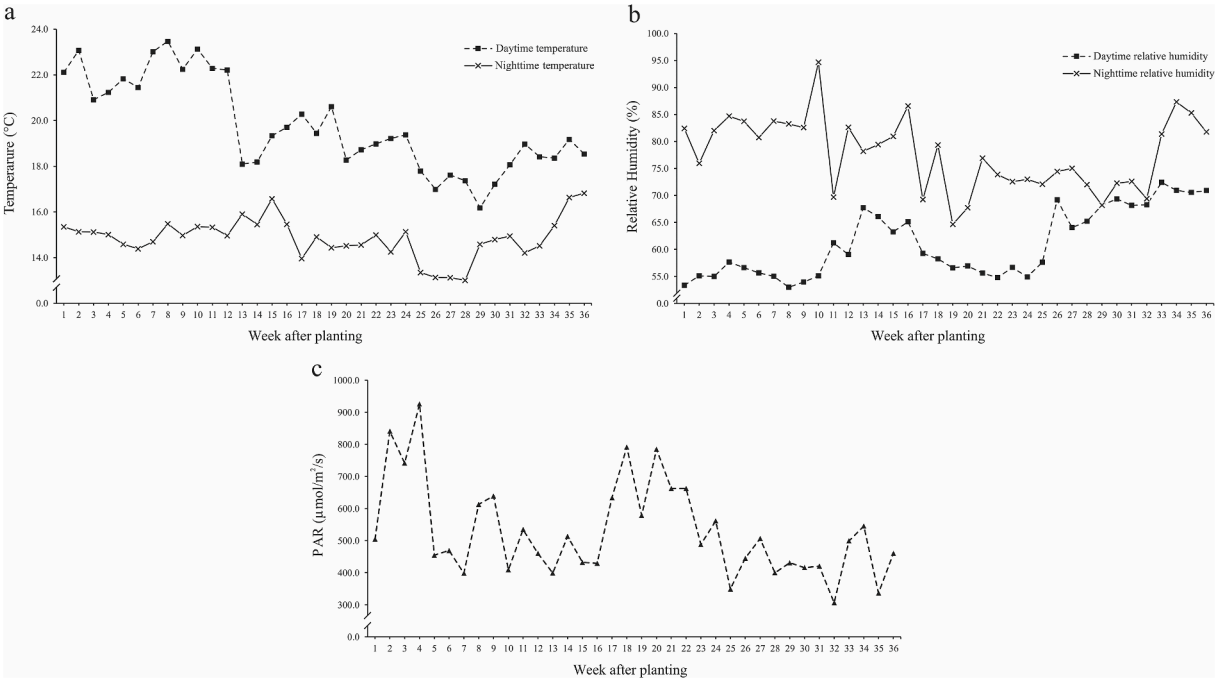

Fig. 1. Weekly temperature (a), relative humidity (b), and photosynthetically active radiation (PAR) (c) recorded during February–October 2021.

Finally, in response to the problem of tomato cultivation under water stress conditions and considering the growing demand of the world population for a sustainable approach to improve food security, the objective of this study was to evaluate the response of tomato plants grafted on wild Solanaceae subjected to water deficit conditions, assessing morpho-physiological parameters during plant growth, yield and fruit quality.

2. Materials and methods

The experiment was conducted at the hydroponic production center of the Universidad Nacional Toribio Rodríguez de Mendoza de Amazonas, Perú (6° 13′ 46″ S, 77° 52′ 21″ W; 2328 *m* asl). A greenhouse (length: 20 *m*, width: 9 *m*, height: 4 *m*) was used with 50 mesh anti-aphid mesh (HPDE) sides and a curved roof covered with 250-μm *anti*-UV film. During the experimental period (February–October 2021), temperature (Daytime: 19.8 ± 2.02 °C; Nighttime: 14.9 ± 0.89 °C) (Fig. 1a), relative humidity (Daytime: 61.1 ± 6.29%; Nighttime: 77.8 ± 6.72%) (Fig. 1b), and photosynthetically active radiation (Fig. 1c) inside the greenhouse were recorded.

2.1. Plant material

Four wild Solanaceae (used as rootstock) were selected from a varied geographical distribution (Table 1). From the identified plants, seeds were collected and immersed in 300 mg l^{-1} of gibberellic acid for 36 h at −10 °C before being sown in 72 cell Plug Trays (4.57 × 4.57 cm cell) filled with peat + perlite (2:1, v:v; pH 6,0 ± 0.5). On the other hand, tomato seeds cv. Rambo F1 germinated under the same conditions, but with a difference of 21 days.

2.2. Micro-grafting and growing conditions

Scion seedlings were either self-grafted or grafted onto wild Solanaceae (Table 1). In a cool environment, the rootstock and scion were joined by the "splice graft" method using a 2.2 mm diameter silicon clip. Micro-grafted seedlings were sprayed with a solution of copper sulfate pentahydrate (2 mL l^{-1}) and benzimidazole (2.5 mL l^{-1}) and maintained at 25 ± 1 °C and 95% relative humidity for the first 14 days, with a photoperiod of 16 h light. Subsequently, they were exposed to indirect light (55% shade) and room temperature for 7 days, with inter-daily foliar applications of 2 mL l^{-1} of Agrostemin®-GL.

To start the experiment, vigorous and uniform grafted plants were selected and transplanted in 8 l bags with substrate composed of burnt rice husk and peat (1:2, v:v) (Table S1), irrigated to field capacity. The nutrient solution used for fertigation was composed of the macro and micronutrients required at each phenological stage of the crop (Table S2). The electrical conductivity of the nutrient solution was 2000 ± 2 μS cm^{-1} at pH 6.0 ± 0.5.

Irrigation treatments based on crop evapotranspiration (ETc) were started 15 days after transplanting [34,35]. Initially, reference evapotranspiration (ET0) in the greenhouse was calculated using CropWat v.8.0 software, with meteorological data obtained from a micro station located inside the greenhouse (temperature, humidity, wind speed, sunshine hours, and radiation) for the last 5 years. ETc was then calculated in a context of optimal fertilization, sanitation and substrate moisture, using the coefficient of consumptive use (Kc) for each phenological stage of tomato (initial 0.60, medium 1.5 and final 0.80) [36]. Irrigation levels were set to meet 100% ETc (high level), 75% ETc (moderate level), 50% ETc (medium level) and 25% ETc (low level). Irrigation was applied using an automated drip system (CHD 2.5 LPH self-compensating dripper) and a timer (Orbit Pocket Star 6 Stations, USA).

The experiment was carried out using a complete randomized design with a 5 × 4 bifactorial arrangement (five rootstocks × four irrigation doses). Each treatment had two replicates with five plants (experimental units) in each replicate.

2.3. Morphological parameters evaluated

After the experiment was established, the following morphological characteristics were determined: plant height (at 168 days), root length, fresh and dry matter of the root and cauline system, rootstock diameter, union diameter, scion diameter and affinity coefficient. To determine the dry matter, the samples were dried in an oven at 80 °C until a constant weight was achieved. The affinity coefficient was determined by the following equation [37]:

$$AC = [C / A \times (C + A) / 2B] \times 10$$

Where, A is the diameter of the scion, B is the diameter of the graft union, C is the diameter of the rootstock. Good affinity is show when AC ≅ 10.

Table 1
Geographical location of wild species of Solanaceae used as rootstocks.

Solanaceae	Geographical coordinates		Elevation
	Latitude South	Longitude West	
Datura stramonium	5° 44' 32.67''	78° 25' 15.55''	466 *m*
Solanum sisymbriifolium	6° 50' 53.88''	78° 01' 1633''	957 *m*
Solanum quitoense	6° 25' 28.76''	77° 30' 41.79''	1565 *m*
Cyphomandra betacea	6° 14' 51.04''	77° 53' 35.28''	2076 *m*

2.4. Physiological parameters evaluated

2.4.1. Relative water content (RWC)

Six leaflets (two per third of the plant) were selected, ten 16 mm discs were immediately extracted from each leaflet and their fresh weight (FW) was recorded. Subsequently, the samples were hydrated in Petri dishes with Milli-Q water for 5 h, surface dried and their turgor weight (TW) was recorded. Finally, the samples were oven dried at 70 °C for a period of 72 h and reweighed to record the dry weight (DW). The RWC was calculated using the equation: RWC (%) = [(FW-DW/TW-DW) x 100] [38].

2.4.2. Relative electrolyte leakage (REL)

Six leaflets were selected from mature leaves, cleaned with Milli-Q water, isolated from the stem and cut into small fragments. Then 0.5 g of tissue was weighed and placed in test tubes with 40 mL of Milli-Q water. These were shaken for 24 h at 250 rpm at room temperature. Subsequently, the first electrical conductivity reading (EC_1) was recorded with a HI 993310 conductivity meter. Then, to allow maximum leakage of ions, they were autoclaved at 120 °C for 20 min, cooled to room temperature and their electrical conductivity (EC_2) was recorded again. REL was determined by the following equation: REL: [EC_1/EC_2 x 100] [39].

2.4.3. Gas exchange, chlorophyll index and leaf water potential

Stomatic conductance (mmol/m^2S), chlorophyll content index (SPAD) and leaf water potential were analyzed at 50, 90 and 168 days, using a SC-1 Leaf Porometer (Decagon Devices, Pullman WA, USA), SPAD-502 chlorophyllometer (Konica Minolta, Tokyo, Japan) and a Scholander-type pressure chamber (PMS-1000, Instrument Company, USA), respectively. Six leaflets were selected from each plant (two per third of the plant) and the average of all measurements was recorded. Readings were taken between 9:00 a.m. and 1:00 p.m.

2.4.4. Photosynthetic pigments and carotenoids

Chlorophyll *a*, *b*, *a*+b and carotenoid contents were determined using a Genesys™ 10 S UV/Vis spectrophotometer (Thermo Scientific™, USA). Pigments were extracted from 0.2 g of fresh leaf tissue. Initially, the samples were crushed in a mortar with 200 mg of magnesium carbonate and 6 mL of acetone (80%). The mixture was transferred to centrifuge tubes covered with aluminum foil and centrifuged at 2500 rpm (10 °C) for 10 min. Finally, an aliquot of 1500 μL (supernatant) was transferred to spectrophotometer tubes for absorbance readings at 663.2; 646.8 and 470 nm. The pigment concentration was translated using the following equations [40]:

Chlorophyll *a* (μg/ml): 12.25 $A_{663,2}$–2.79 $A_{646,8}$

Chlorophyll *b* (μg/ml): 21.50 $A_{646,8}$–5.10 $A_{663.2}$

Chlorophyll *a*+b (μg/ml): Chlorophyll *a* + Chlorophyll *b*

Carotenoid (μg/ml): (1000 A_{470} – 1.82 C_a – 85.02 C_b)/198

2.4.5. Stomatic index and density

Using a thin layer of translucent enamel, 10 impressions (abaxial surface free of veining) were obtained from 4 leaflets of 2 leaves selected from the apical third. The specimens were placed on a slide, stained with toluidine blue and fixed with Canada balsam, then observed and photographed with a microscope (Leica DM2000 LED, Leica, Germany) equipped with a digital camera (Leica MC170 HD, Leica, Germany). In each optical field (100× magnification) the number of stomata (NS) and epidermal cells (EC) were counted. The stomata index (SI) was calculated using the following equation: SI = [(NS/(EC + NS)] *100 [41]. Stomatic density was determined in an area of 1 mm^2 using a Neubauer chamber.

2.5. Biochemical parameters

The samples (fruits, leaves, and root) were chopped and frozen at −80 °C for 24 h. Subsequently, they were freeze-dried for 72 h at a pressure of 0.003 mbar (Labconco, Free Zone, 4.5 l, - 84 °C, USA). Finally, these were crushed and sieved (75 μm).

2.5.1. Total proline content

500 mg of tissue sample (leaf and root) was mixed with 5 mL of 3% aqueous sulfosalicylic acid in a 15 mL falcon tube and centrifuged at 300 rpm for 60 min at room temperature. Subsequently, a second centrifugation was performed at 10 000 rpm for 30 min at 4 °C. Next, 2000 μL of supernatant, 2000 μL of acid ninhydrin (0.1 M) and 2.0 mL glacial acetic acid (hot) were added in glass tubes (covered with aluminum foil) and homogenized for 1 min in a vortex. The mixture was left in boiling water for 60 min before being placed on ice for 15 min. Finally, 3 mL of toluene was added, stirred for 1 min, and then allowed to stand for 10 min until phase separation. The absorbance reading was taken at 520 nm. l-proline was used to create the calibration curve [42]. The proline content was calculated by interpolating the absorbance of the sample on the calibration curve.

Table 2
Effect of interaction of water regimes and rootstocks on plant height and biomass.

Parameters	Rootstock ®	Irrigation amount (I)				Analysis of Variance			Coefficient of variation (%)
		100% *Etc*	75% *Etc*	50% *Etc*	25% *Etc*	R	I	R × I	
Plant height (cm)	*S. licopersicum* (self-graft)	89.10 ± 0.39 b	80.50 ± 0.54 d	71.25 ± 1.10 fg	63.58 ± 0.67 k	***	***	***	0.81
	D. stramonium	90.87 ± 0.26 a	88.97 ± 0.29 b	71.88 ± 0.59 f	68.27 ± 0.40 hi				
	C. betacea	70.57 ± 0.74 g	69.32 ± 0.71 h	66.13 ± 0.55 j	57.95 ± 0.92 l				
	S. quitoens	68.08 ± 0.33 i	58.93 ± 0.54 l	49.92 ± 0.29 *m*	48.43 ± 0.45 n				
	S. sisymbriifolium	88.92 ± 0.44 b	84.38 ± 0.55 c	78.30 ± 0.57 e	67.18 ± 0.54 ij				
Root length (cm)	*S. licopersicum* (self-graft)	60.92 ± 0.59 b	51.05 ± 0.48 f	48.35 ± 0.85 g	42.33 ± 0.41 h	***	***	***	1.22
	D. stramonium	66.52 ± 0.61 a	61.00 ± 0.63 b	56.92 ± 0.76 d	52.38 ± 0.47 e				
	C. betacea	41.42 ± 0.54 h	39.63 ± 0.58 i	26.03 ± 0.39 j	20.22 ± 0.32 k				
	S. quitoens	13.78 ± 0.22 n	16.22 ± 0.59 *m*	17.58 ± 0.26 l	18.40 ± 0.15 l				
	S. sisymbriifolium	60.07 ± 0.29 b	58.05 ± 0.38 c	53.03 ± 0.73 e	49.42 ± 0.50 g				
Root fresh matter (g)	*S. licopersicum* (self-graft)	125.34 ± 1.27 f	101.20 ± 1.11 g	89.18 ± 1.05 h	70.83 ± 1.43 j	***	***	***	1.46
	D. stramonium	191.01 ± 1.19 a	140.32 ± 0.86 d	100.37 ± 1.10 g	98.63 ± 0.82 g				
	C. betacea	75.52 ± 0.92 i	39.62 ± 1.30 k	27.09 ± 0.86 l	10.04 ± 0.42 o				
	S. quitoens	11.74 ± 0.77 o	18.51 ± 0.50 n	20.26 ± 0.73 mn	22.34 ± 0.54 *m*				
	S. sisymbriifolium	177.67 ± 0.96 b	154.09 ± 1.39 c	136.66 ± 3.51 e	98.92 ± 0.81 g				
Root dry matter (g)	*S. licopersicum* (self-graft)	21.84 ± 0.84 e	16.96 ± 1.24 fgh	13.97 ± 0.59 i	12.17 ± 0.46 jk	***	***	***	3.86
	D. stramonium	36.25 ± 0.65 a	28.12 ± 0.63 d	18.12 ± 0.94 f	15.74 ± 0.72 h				
	C. betacea	15.81 ± 0.48 gh	12.19 ± 0.62 jk	10.81 ± 0.14 kl	7.96 ± 0.61 *m*				
	S. quitoens	13.34 ± 0.47 ij	10.05 ± 0.58 l	8.17 ± 0.50 *m*	3.66 ± 0.48 n				
	S. sisymbriifolium	33.12 ± 0.57 b	29.74 ± 0.43 c	22.00 ± 0.99 e	17.18 ± 0.65 fg				
Fresh matter of the aerial part (g)	*S. licopersicum* (self-graft)	2492.6 ± 31.53 d	1997.68 ± 17.5 g	830.71 ± 46.81 l	524.66 ± 67.89 n	***	***	***	2.12
	D. stramonium	3926.18 ± 43.01 a	3240.11 ± 34.00 b	2218.94 ± 42.90 f	987.55 ± 6.76 jk				
	C. betacea	995.46 ± 1.93 j	920.37 ± 1.05 k	692.82 ± 73.28 *m*	382.05 ± 4.00 o				
	S. quitoens	1193.19 ± 3.27 i	995.63 ± 2.93 j	754.96 ± 3.18 *m*	441.93 ± 0.79 o				
	S. sisymbriifolium	2891.75 ± 8.72 c	2347.41 ± 32.54 e	1751.93 ± 36.01 h	930.61 ± 1.04 jk				
Dry matter of the aerial part (g)	*S. licopersicum* (self-graft)	172.90 ± 1.13 d	118.86 ± 0.42 g	85.82 ± 0.69 k	74.26 ± 0.46 *m*	***	***	***	0.96
	D. stramonium	218.02 ± 0.60 a	199.18 ± 0.60 b	173.84 ± 0.61 d	90.97 ± 0.52 j				
	C. betacea	98.99 ± 0.40 h	76.48 ± 0.71 lm	51.30 ± 0.37 o	33.37 ± 0.55 p				
	S. quitoens	123.04 ± 1.37 f	88.61 ± 0.99 j	78.20 ± 0.60 l	54.27 ± 0.49 n				
	S. sisymbriifolium	190.29 ± 1.18 c	173.12 ± 0.77 d	146.71 ± 3.45 e	93.37 ± 1.89 i				

Values (±SD) not followed by same letter denote significant differences between treatments (DGC test at $p \leq 0.05$). Significance levels *, **, *** correspond to $p \leq 0.05$, 0.01 and 0.001, respectively.

2.6. Yield and fruit quality parameters

The number of flower clusters per plant, flowers per cluster and commercially viable fruit (>50 g) per plant were recorded during the first 90 days after installation. Also, the total weight of harvested fruit (per plant) during the entire production period was used to calculate the total cumulative yield (kg/plant) at 168 days, which was related to the amount of water used to calculate productivity according to irrigation frequency (kg/m^2).

To determine the longitudinal and transverse diameter, a total of ten commercial fruits were randomly selected. Fruit firmness was measured with a GY-4 digital penetrometer (Roweeltec, China) equipped with a 7 mm conical tip, and the average of 3 equatorial measurements per fruit was recorded. Total soluble solids (°Brix) were measured at room temperature using a Pocket PAL-1 digital refractometer (Atago, Japan). The pH of the fruit extract was measured with a HANNA HI2211 potentiometer (Hanna, USA). Titratable acidity was expressed as the percentage of citric acid equivalents in the fruit juice; for this purpose, 10 g of juice was extracted and mixed with 50 mL of distilled water before being filtered. This was titrated with 0.1 N NaOH to a pH of 8.2. The volume spent was multiplied by a correlation factor of 0.064.

2.6.1. Total phenolic content

This was determined following the procedures of [43]. 1 g of lyophilized fruit was mixed with 10 mL of methanol (80%), then centrifuged at 400 rpm for 16 h. Subsequently, a second centrifugation was performed at 5000 rpm for 15 min. Then, 1000 μL of supernatant and 2500 μL of 10% (w/v) Folin-Ciocalteu were added in glass tubes (covered with aluminum foil). After 5 min, 2000 μL of 75% Na_2CO_3 was added and incubated at 50 °C for 10 min. Finally, the absorbance of the sample was measured at 760 nm. The calibration curve was created with dilutions (0–200 mg l^{-1}) of aqueous gallic acid (GAE), generating the following equation: $Y = 0.011x + 0.08$, $R^2 = 0.996$. The results were expressed as mg EAG/100 g FL.

2.7. Anatomical and histological observation of the graft

Samples were collected 2 cm in length above and below the graft junction and immediately cut longitudinally and transversely for anatomical characterization of the graft junction.

Histological takes were developed using the methodology of [44]. The samples were immersed in 90 mL of 70° ethyl alcohol plus 5 mL of formaldehyde and 5 mL of glacial acetic acid for 72 h. After that, they were immersed in 50% glacial acetic acid for 48 h. They were then passed through a series of increasing concentrations of ethyl alcohol (35, 50, 70, 85, 96 and 100%) over the course of 8 days. Tissue diaphanization was performed in xylol for 8 days and kerosene embedding for one week at 65 °C. Subsequently, 20 μm slices were made (Leica RM2125 RTS microtome, Germany) and expanded in a water bath at 30 °C to be contained in a slide and deparaffinized in xylol. The sections were soaked in decreasing concentrations of alcohol (100 - 70%) for 5 min, and then stained with acid fuchsin (0.1% w/v) followed by toluidine blue (0.05% w/v). Finally, they were dehydrated in 70, 96 and 100% alcohol for 5 min each and rinsed in xylol for the same time. Samples were fixed with Canada balsam, then observed and photographed under a stereomicroscope at 40 × (Leica S9i, Germany).

2.8. Statistical analysis

The data were subjected to two-way analysis of variance, and the means of the variables that were statistically significant were compared using the Di Rienzo, Guzman and Casanoves (DGC) multiple comparisons test. The analysis was performed using InfoStat software version 2017. To observe the correlation of the set of parameters evaluated, the Pearson test was performed ($P \leq 0.05$).

3. Results

3.1. Morphological parameters

According to two-way ANOVA, water deficit and rootstock, both individually and combined, significantly affected tomato scion morphological characteristics (Table 2). As expected, tomato growth and development were influenced by water availability; that is, water limitation (under irrigation - 25% ETc) significantly decreased plant growth compared to higher water supply (100% ETc), regardless of the rootstock used (Table 2). The rootstock × 100% ETc interaction led to plants reaching greater height and root length than their peers under a different irrigation regime; however, it was interesting to note that scions grafted on rootstocks of *D. stramonium* (88.97 ± 0.29 cm height; 61.00 ± 0.63 cm root length) and *S. sisymbriifolium* (88.92 ± 0.44 cm height; 60.07 ± 0.29 cm root length) irrigated to satisfy 75% of ETc reached values that were statistically equal to those of self-grafted tomato plants (89.10 ± 0.39 cm height; 60.92 ± 0.59 cm root length) irrigated to satisfy 100% of ETc. Biomass values were in line with the development recorded by the plant (Table 2).

On the other hand, using the "Branas" coefficient, it can be said that among the wild Solanaceae used as rootstock, *D. stramonium* has the best affinity, with a coefficient ≅ 10 between rootstock diameter, union diameter, scion diameter (Table S3).

3.2. Physiological and biochemical parameters

The results of the analysis of variance showed that the factors (water deficit and rootstock) and their interactions had significant

effects on all physiological and biochemical characteristics evaluated. The values of chlorophyll index, stomatal conductance and water potential were sensitive to the level of irrigation in the different growth stages, reaching a higher level in plants irrigated to satisfy 100% of ETc and gradually decreasing with the change of irrigation regime (Fig. 2). The average value of chlorophyll index at vegetative stage, flowering stage and production stage ranged from 41.69 to 48.83, 45.07 to 69.98 and 44.55 to 77.18, respectively, throughout the tomato growth stage (Fig. 2a).

The results of stomatal conductance have shown that scions grafted on *S. sisymbriifolium* had a higher record throughout the evaluation period. However, it is important to note that the behavior of the results at the rootstock level shows logically favorable values with increasing irrigation applied (Fig. 2b). On the other hand, it was observed that self-grafted plants were more sensitive to water deficit, with water potential ranging from -1.11 ± 0.04 (high irrigation level - 100% ETc) to -2.27 ± 0.05 (low irrigation level - 25% ETc) MPa during the production stage. In contrast, it was observed that scions grafted on *D. stramonium* had the highest water potential values, implying that this wild Solanaceae is better adapted to low soil water availability (Fig. 2c).

When comparing the concentration of photosynthetic pigments, it was observed that, independently of the rootstock, there is a directly proportional relationship between the irrigation regime and the chlorophyll and carotenoid content. Total chlorophyll content was higher in scions grafted on *S. quitoens*, followed by *D. stramonium*, at each irrigation level evaluated (Table 3).

The results on relative water content show that the water status of the plants was influenced by the irrigation regime. At the rootstock level, both *D. stramonium* and *S. sisymbriifolium*, even with medium irrigation (50% ETc), showed values of relative water content comparable or better than those of other plants established with higher water supply (Table 3). On the other hand, it can be observed that *D. stramonium* is the species that best tolerates water deficit stress, registering a significantly lower electrolyte loss for a low irrigation level (25% ETc). Finally, it is important to note that stomatal index and density followed the same trend as parameters such as photosynthetic pigment content (Table 3).

Fig. 2d shows the results of proline accumulation in leaves and roots. Subjecting plants to growth under water deficit conditions resulted in an increase in proline content at the root and leaf levels. Scions grafted on *S. quitoense* and *D. stramonium* showed lower proline biosynthesis at the foliar level at all four irrigation levels. At the root level, *D. stramonium* rootstocks showed lower proline biosynthesis at all four irrigation levels. The highest proline biosynthesis was found in self-grafted tomato plants.

3.3. Fruiting characteristics, productivity, and quality of the fruit

Water deficit, rootstock and their interaction significantly affected the results of yield and fruit quality related parameters shown in

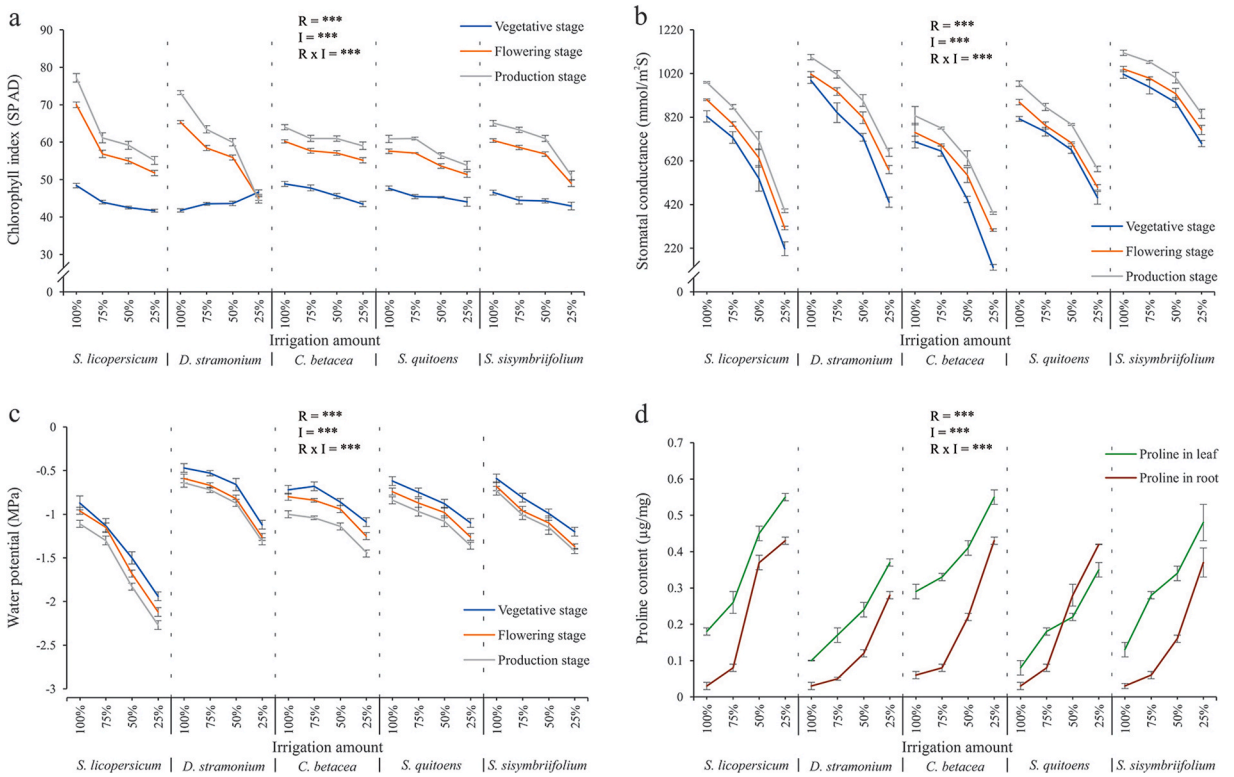

Fig. 2. Effect of interaction of water regimes and rootstocks on (a) chlorophyll index, (b) stomatal conductance, (c) water potential, and (d) proline content. Significant effects of the factors rootstock (R), irrigation amount (I), and the interactions (R × I) are given in the figure: ns, not significant; *, $P < 0.05$; **, $P < 0.01$; and ***, $P < 0.001$.

Table 3
Effect of interaction of water regimes and rootstocks on photosynthetic pigment content, stomatal index, stomatal density, relative water content and relative electrolyte leakage.

Parameters	Rootstock ®	Irrigation amount (I)				Analysis of Variance			Coefficient of variation (%)
		100% *Etc*	75% *Etc*	50% *Etc*	25% *Etc*	R	I	R × I	
Chlorophyll *a* (µg/ml)	*S. licopersicum* (self-graft)	44.38 ± 0.13 d	29.60 ± 0.05 h	20.29 ± 0.01 *m*	12.07 ± 0.01 q	***	***	***	0.22
	D. stramonium	46.83 ± 0.08 b	36.66 ± 0.05 e	19.06 ± 0.04 n	12.55 ± 0.11 p				
	C. betacea	30.54 ± 0.04 f	30.20 ± 0.03 g	28.71 ± 0.04 k	7.24 ± 0.03 r				
	S. quitoens	47.46 ± 0.10 a	45.26 ± 0.06 c	28.98 ± 0.04 i	28.84 ± 0.07 j				
	S. sisymbriifolium	28.90 ± 0.03 j	23.77 ± 0.02 l	16.24 ± 0.07 o	5.38 ± 0.01 s				
Chlorophyll *b* (µg/ml)	*S. licopersicum* (self-graft)	30.39 ± 0.05 b	26.49 ± 0.07 e	10.34 ± 0.05 n	6.51 ± 0.02 q	***	***	***	0.31
	D. stramonium	29.83 ± 0.04 c	28.92 ± 0.08 d	12.64 ± 0.04 *m*	10.21 ± 0.14 o				
	C. betacea	20.42 ± 0.07 h	19.90 ± 0.05 j	19.15 ± 0.03 k	6.38 ± 0.07 r				
	S. quitoens	30.63 ± 0.07 a	30.64 ± 0.07 a	25.43 ± 0.04 f	23.48 ± 0.06 g				
	S. sisymbriifolium	20.33 ± 0.02 i	12.76 ± 0.01 l	9.41 ± 0.03 p	3.71 ± 0.01 s				
Chlorophyll *a* + b (µg/ml)	*S. licopersicum* (self-graft)	74.77 ± 0.14 d	56.09 ± 0.10 f	30.63 ± 0.05 o	18.58 ± 0.02 r	***	***	***	0.22
	D. stramonium	76.66 ± 0.11 b	65.58 ± 0.10 e	31.70 ± 0.08 n	22.75 ± 0.25 q				
	C. betacea	50.95 ± 0.07 i	50.11 ± 0.06 j	47.86 ± 0.05 l	13.62 ± 0.10 s				
	S. quitoens	78.09 ± 0.15 a	75.90 ± 0.11 c	54.41 ± 0.08 g	52.32 ± 0.09 h				
	S. sisymbriifolium	49.23 ± 0.02 k	36.54 ± 0.01 *m*	25.65 ± 0.09 p	9.08 ± 0.01 t				
Carotenoids (µg/ml)	*S. licopersicum* (self-graft)	15.00 ± 0.01 a	14.43 ± 0.05 c	7.78 ± 0.07 k	0.14 ± 0.03 p	***	***	***	0.85
	D. stramonium	14.69 ± 0.05 b	13.78 ± 0.05 d	2.83 ± 0.06 *m*	1.63 ± 0.28 n				
	C. betacea	10.74 ± 0.02 g	10.53 ± 0.03 h	10.03 ± 0.09 i	7.80 ± 0.02 k				
	S. quitoens	8.28 ± 0.03 j	7.26 ± 0.03 l	1.56 ± 0.05 n	0.80 ± 0.04 o				
	S. sisymbriifolium	13.79 ± 0.02 d	13.00 ± 0.03 e	12.39 ± 0.01 f	9.96 ± 0.04 i				
Relative electrolyte leakage (µs/cm)	*S. licopersicum* (self-graft)	18.07 ± 0.35 o	22.92 ± 0.77 *m*	30.14 ± 0.51 j	35.43 ± 0.75 h	***	***	***	1.91
	D. stramonium	21.33 ± 0.43 n	26.62 ± 0.79 k	29.24 ± 0.54 j	33.48 ± 0.63 i				
	C. betacea	25.33 ± 0.98 l	29.80 ± 0.36 j	38.04 ± 0.58 g	43.30 ± 0.92 e				
	S. quitoens	46.13 ± 0.80 d	52.09 ± 0.78 c	79.21 ± 0.57 b	88.29 ± 0.94 a				
	S. sisymbriifolium	21.84 ± 0.85 n	25.98 ± 0.83 k	35.80 ± 0.62 h	41.46 ± 0.79 f				
Relative áter content (%)	*S. licopersicum* (self-graft)	88.50 ± 0.98 f	81.44 ± 0.68 h	75.24 ± 0.64 k	66.11 ± 0.34 n	***	***	***	0.86
	D. stramonium	98.49 ± 0.90 a	92.62 ± 0.65 c	88.25 ± 0.92 f	79.58 ± 0.56 i				
	C. betacea	89.51 ± 0.63 e	83.03 ± 0.77 g	76.49 ± 0.83 j	70.53 ± 0.48 *m*				
	S. quitoens	96.03 ± 0.62 b	87.50 ± 1.07 f	81.54 ± 0.85 h	74.02 ± 0.43 l				
	S. sisymbriifolium	99.22 ± 0.50 a	98.27 ± 0.59 a	90.82 ± 0.66 d	82.82 ± 0.94 g				
Stomatal index	*S. licopersicum* (self-graft)	21.25 ± 0.46 a	16.51 ± 1.15 c	13.72 ± 0.56 e	11.70 ± 0.46 g	***	***	***	5.19
	D. stramonium	17.19 ± 0.91 b	16.08 ± 0.69 c	15.61 ± 0.72 d	12.96 ± 0.65 f				

(*continued on next page*)

Table 3 (*continued*)

Parameters	Rootstock ®	Irrigation amount (I)				Analysis of Variance			Coefficient of variation (%)
		100% *Etc*	75% *Etc*	50% *Etc*	25% *Etc*	R	I	R × I	
Stomatal density (mm^2)	*C. betacea*	17.97 ± 0.62 b	15.11 ± 0.52 d	14.04 ± 0.71 e	13.02 ± 0.51 f	***	***	***	1.22
	S. quitoens	15.17 ± 0.88 d	14.37 ± 0.80 e	13.55 ± 0.83 e	12.30 ± 0.81 f				
	S. sisymbriifolium	15.11 ± 0.81 d	15.05 ± 0.68 d	14.03 ± 1.12 e	12.67 ± 1.04 f				
	S. licopersicum (self-graft)	7.64 ± 0.33 a	5.99 ± 0.81 b	5.89 ± 0.18 b	4.06 ± 0.39 d				
	D. stramonium	6.28 ± 0.54 b	5.64 ± 0.49 b	4.86 ± 0.35 c	4.74 ± 0.25 c				
	C. betacea	4.90 ± 0.78 c	4.48 ± 0.70 c	3.93 ± 0.47 d	4.00 ± 0.18 d				
	S. quitoens	5.29 ± 0.45 c	4.13 ± 0.61 d	3.96 ± 0.32 d	3.61 ± 0.33 d				
	S. sisymbriifolium	3.05 ± 0.24 e	3.78 ± 0.34 d	3.78 ± 0.70 d	3.50 ± 0.33 d				

Values (±SD) not followed by same letter denote significant differences between treatments (DGC test at $p \leq 0.05$). Significance levels *, **, *** correspond to $p \leq 0.05$, 0.01 and 0.001, respectively.

Tables 4 and 5, respectively. The use of *D. stramonium* as rootstock allowed recording a higher number of floral clusters (18.50 ± 0.55) as well as flowers per cluster (19.50 ± 0.55), resulting in a higher number of commercially valuable fruits (42.83 ± 1.47) and, as a result, a higher yield per plant (8.14 ± 0.65 kg) (Table 4). In addition, this rootstock allowed recording fruits with the best longitudinal diameter (75.25 ± 1.11 mm) and mean diameter (67.13 ± 1.90 mm). It is important to note that these results were obtained with optimum water supply (100% ETc) and decreased progressively when the irrigation regime was reduced; however, in all situations, they were superior to the other treatments evaluated. The productivity of irrigation water is directly proportional to the yield achieved, i.e. a downward trend is observed when limiting the availability of applied water. All the parameters mentioned above were calculated using data collected from the second to the tenth productive bunch of each plant.

Regarding fruit quality, the results show that rootstock and irrigation regimes have a significant impact on the characteristics measured (Table 5). When the irrigation level was reduced, total soluble solids (°Brix) showed a tendency to increase. At all four irrigation levels, self-grafted tomato fruit had the highest concentration of total soluble solids, while scions grafted on *S. quitoens* had the lowest. Fruit pH ranged from 3.58 ± 0.36 to 4.69 ± 0.06. Fruit firmness "hardness" increased as the amount of irrigation provided decreased, with fruit obtained from scions grafted on *C. betacea* reaching the lowest levels with a maximum of 26.84 ± 0.64 N at a low irrigation level (25% ETc). Finally, *D. stramonium* and *S. sisymbriifolium* rootstocks were distinguished by showing a slight increase in total phenolic content of the fruit when grown under moderate irrigation (75% ETc) compared to high irrigation (100% ETc).

3.4. Correlation analysis

Fig. 3 illustrates the linear dependence between morphological, physical and biochemical parameters of the plants. The results of the correlation analysis showed that the cumulative yield per plant showed a strong positive correlation with the number of commercially valuable fruits ($r = 0.950$), relative water content ($r = 0.909$) and biomass-related parameters. In addition, it had a moderate positive correlation with photosynthetic pigment content, stomatal index ($r = 0.548$) and root length ($r = 0.493$). Cumulative yield was found to be strongly negatively correlated with water potential ($r = -0.062$), moderately correlated with leaf proline content ($r = -0.491$) and weakly correlated with root proline content ($r = -0.830$). Total soluble solids were negatively correlated with water potential ($r = -0.078$).

3.5. Internal characterization and anatomical observation of the graft union

Callus volume at the graft union varied markedly depending on the species interacting with the scion (Fig. 4). Autograft (Fig. 4a) and *D. stramonium* rootstock (Fig. 4b) were found to form barely noticeable callus, while the other species caused greater hypertrophy development (Fig. 4 *c*-e). Callus growth was observed to have an impact on both graft functionality and adherence, exhibiting a high incidence of necrotic layers (dead cells). The use of *S. sisymbriifolium* (Fig. 4c), *S. quitoens* (Fig. 4d), and *C. betacea* (Fig. 4e) rootstocks caused the scions to exhibit increased adventitious root formation near the graft union.

For the anatomical analysis of the graft union according to the amount of irrigation, the tomato/*D. stramonium* combination was selected as the scion/rootstock interaction with the best compatibility (except for the autograft) (Fig. 5). It is observed that when the irrigation regime is reduced, there is a better vascular connection (Fig. 5c and d), since the interior of the interface is replaced by callus tissue (medium irrigation - 50% ETc and low 25% ETc). On the contrary, when the water supply is higher than 75% of ETc, necrotic tissue and empty spaces between the graft and the rootstock interface are observed (Fig. 5a and b).

Table 4
Effect of interaction of water regimes and rootstocks on fruiting characteristics and productivity of tomato.

Parameters	Rootstock ®	Irrigation amount (I)				Analysis of Variance			Coefficient of variation (%)
		100% *Etc*	75% *Etc*	50% *Etc*	25% *Etc*	R	I	R × I	
Number of flower clusters per plant	*S. licopersicum* (self-graft)	12.17 ± 0.75 f	11.33 ± 0.52 f	8.50 ± 0.55 i	4.50 ± 0.55 k	***	***	***	5.06
	D. stramonium	18.50 ± 0.55 a	16.00 ± 0.89 c	16.33 ± 0.52 c	9.50 ± 0.55 h				
	C. betacea	11.67 ± 0.52 f	8.50 ± 0.55 i	6.67 ± 0.82 j	3.17 ± 0.41 l				
	S. quitoens	13.33 ± 0.52 e	11.50 ± 0.55 f	10.50 ± 0.55 g	8.83 ± 0.41 i				
	S. sisymbriifolium	17.33 ± 0.52 b	15.50 ± 0.55 c	14.33 ± 0.52 d	9.33 ± 0.52 h				
Number of flowers per cluster	*S. licopersicum* (self-graft)	15.83 ± 0.41 c	15.33 ± 0.52 c	14.50 ± 0.55 d	4.67 ± 0.52 l	***	***	***	5.10
	D. stramonium	19.50 ± 0.55 a	17.83 ± 0.75 b	10.83 ± 0.75 g	8.50 ± 0.55 i				
	C. betacea	12.50 ± 0.55 f	10.00 ± 0.63 h	6.50 ± 0.55 k	3.83 ± 0.75 *m*				
	S. quitoens	15.50 ± 0.55 c	14.50 ± 0.55 d	12.17 ± 0.75 f	6.00 ± 0.89 k				
	S. sisymbriifolium	18.33 ± 0.52 b	15.83 ± 0.75 c	13.50 ± 0.55 e	7.50 ± 0.55 j				
Number of marketable fruits per plant	*S. licopersicum* (self-graft)	31.17 ± 0.75 d	24.50 ± 0.55 h	12.33 ± 0.52 k	4.50 ± 0.55 n	***	***	***	3.69
	D. stramonium	42.83 ± 1.47 a	40.67 ± 1.03 b	25.67 ± 0.82 g	8.33 ± 0.52 *m*				
	C. betacea	25.67 ± 0.82 g	19.33 ± 1.03 j	9.50 ± 0.55 l	2.50 ± 0.55 o				
	S. quitoens	31.33 ± 1.21 d	28.33 ± 0.82 f	22.83 ± 0.75 i	7.33 ± 1.03 *m*				
	S. sisymbriifolium	41.00 ± 0.89 b	39.33 ± 0.52 c	29.67 ± 0.82 e	7.67 ± 0.82 *m*				
Longitudinal fruit diameter (mm)	*S. licopersicum* (self-graft)	61.51 ± 1.67 e	51.03 ± 1.66 i	37.94 ± 1.17 l	29.38 ± 0.48 n	***	***	***	1.98
	D. stramonium	75.25 ± 1.11 a	66.51 ± 1.06 c	53.55 ± 1.17 h	36.17 ± 0.44 *m*				
	C. betacea	55.45 ± 0.66 g	51.83 ± 0.83 i	48.16 ± 0.47 j	37.71 ± 1.15 l				
	S. quitoens	63.52 ± 0.75 d	58.46 ± 1.13 f	51.82 ± 0.98 i	42.95 ± 1.09 k				
	S. sisymbriifolium	69.08 ± 0.86 b	62.16 ± 0.54 e	53.16 ± 1.51 h	38.03 ± 0.53 l				
Transversal fruit diameter (mm)	*S. licopersicum* (self-graft)	56.85 ± 0.61 b	43.40 ± 1.03 e	36.08 ± 1.77 g	26.59 ± 0.58 i	***	***	***	3.15
	D. stramonium	67.13 ± 1.90 a	52.76 ± 1.08 c	44.30 ± 1.96 e	29.97 ± 0.40 h				
	C. betacea	46.38 ± 1.11 d	46.34 ± 1.10 d	39.41 ± 0.46 f	31.11 ± 0.69 h				
	S. quitoens	55.75 ± 2.06 b	46.70 ± 1.02 d	47.29 ± 2.82 d	35.00 ± 2.21 g				
	S. sisymbriifolium	66.41 ± 0.86 a	52.99 ± 1.60 c	46.74 ± 0.84 d	30.04 ± 1.13 h				
Accumulated yield per plant (kg)	*S. licopersicum* (self-graft)	4.78 ± 0.14 f	4.01 ± 0.06 g	2.91 ± 0.17 i	0.75 ± 0.05 l	***	***	***	8.24
	D. stramonium	8.14 ± 0.65 a	6.70 ± 0.41 c	5.19 ± 0.67 e	2.69 ± 0.13 i				
	C. betacea	3.47 ± 0.21 h	3.06 ± 0.11 i	1.79 ± 0.20 j	0.35 ± 0.05 *m*				
	S. quitoens	5.84 ± 0.17 d	4.56 ± 0.50 f	3.79 ± 0.23 g	1.23 ± 0.06 k				
	S. sisymbriifolium	7.14 ± 0.65 b	6.07 ± 0.08 d	3.98 ± 0.28 g	1.93 ± 0.21 j				
Irrigation water productivity (kg/m^3)	*S. licopersicum* (self-graft)	37.23 ± 0.59 e	33.60 ± 0.91 f	28.19 ± 0.82 h	19.16 ± 0.43 j	***	***	***	4.13
	D. stramonium	54.95 ± 2.85 a	42.79 ± 2.98 c	28.34 ± 1.33 h	19.35 ± 0.46 j				
	C. betacea								

(*continued on next page*)

Table 4 (*continued*)

Parameters	Rootstock ®	Irrigation amount (I)				Analysis of Variance			Coefficient of variation (%)
		100% *Etc*	75% *Etc*	50% *Etc*	25% *Etc*	R	I	R × I	
		31.97 ± 1.20 g	29.02 ± 0.70 h	17.44 ± 0.54 k	12.49 ± 0.45 l				
	S. quitoens	39.83 ± 1.02 d	30.80 ± 1.33 g	27.00 ± 1.12 h	16.86 ± 0.87 k				
	S. sisymbriifolium	50.78 ± 1.34 b	42.69 ± 0.80 c	23.97 ± 0.56 i	17.99 ± 0.42 k				

Values (±SD) not followed by same letter denote significant differences between treatments (DGC test at $p \leq 0.05$). Significance levels *, **, *** correspond to $p \leq 0.05$, 0.01 and 0.001, respectively.

4. Discussions

The use of rootstocks that can reduce the effects of water stress represents a viable opportunity to take advantage of the promising characteristics of the diversity of wild Solanaceae [45]. However, the plant response to a water deficit is a complex process involving morpho-physiological and biochemical changes that vary according to the type of crop, as well as the duration and severity of the stress [46].

In this study, numerous morphological, physiological, and biochemical changes were observed during the course of the irrigation treatment; however, the rootstock used had a considerable effect on scion perception and tolerance to stress. Overall, tomato plants grafted with *D. stramonium* exhibited greater tolerance to water deficiency stress, maintaining better performance in terms of growth, biomass, water potential, photosynthetic pigments, relative water content, electrolyte loss, proline biosynthesis and other parameters, compared to tomato plants grafted with *C. betacea*, *S. quitoens*, *S. sisymbriifolium* and self-grafted.

The ability of the rootstock to enhance nutrient and water uptake from the soil is a characteristic that is related to how well the scion adapts to or tolerates stress situations [47,48], as the scion can use these resources to counteract the effects of stress caused, for example, by a water deficit [49]. In fact, the *D. stramonium* rootstock showed a better developed root system compared to the other treatments evaluated. As a result, rootstock selection based on root characteristics may influence scion growth because of its relationship with water and nutrient absorption capacity [25,50,51]. However, it is also vital to select scions of high compatibility that can provide a higher ration of assimilates to the rootstocks (through photosynthesis) to build a root system that allows the search for water in all directions of the soil or substrate [52–54]. In addition, the activation of the graft repair mechanisms implies an important metabolic demand in the junction zone that can be covered by the photochemical activity of the scion throughout its phenological cycle [55].

Grafting is a historically validated technology that is still used in agricultural practices due to its effectiveness and usefulness in improving agronomic characteristics [56]. This technique allows the plant to perform better in morpho-physiological aspects and even overcome stress-related conditions [25,57–60], as well as potentially improve yield and fruit quality [59,61]. However, the procedures involve technical difficulties due to the compatibility between plants to be grafted, since a low affinity in the rootstock-scion combination can lead to slow growth and, in some cases, lower yields [62], due to vascular combinations not completing the healing/scioning process [57]. Analysis of the internal anatomy of the graft union revealed that graft healing varies among rootstocks, with the presence of necrotic tissues. Necrotic areas indicate incomplete vascular connections at the graft union [37], originating localized cell death, alteration of the vascular system and loss of water and solutes [55]. Therefore, the distribution of vascular meristematic tissue in the scion and rootstock is essential for the correct establishment of the graft [63]. This study found low compatibility with rootstocks of *C. betacea*, *S. quitoense* and *S. sisymbriifolium*. On the contrary, the use of *D. stramonium* allowed greater growth and accumulation of fresh and dry matter in the scions, indicating that it generates a tolerance response to water deficit. As a result, it can be said that tolerating water deficit stress is an adaptive response that depends mainly on the rootstock (S [24,25].

Stress induced by lack of water directly modifies the chemical composition and physical structure of the cell membrane as it disintegrates due to lipid peroxidation [64]. Lack of water accelerates the degradation of photosynthetic pigments as a result of the deterioration of the thylakoid membranes, which serve as the structural basis for the absorption, translocation and transformation of light in chloroplasts [65]. In other words, the main process affected by water deficit is photosynthesis [46]. The current study found that the use of *D. stramonium* as rootstock allowed the scion cauline system to maintain a high level of photosynthetic pigments. This response may be related to the fact that *D. stramonium* is a species with high water uptake and nutrient translocation capacity [66], which allows the scion to utilize solar energy more efficiently during photosynthesis [65].

Under unfavorable growth conditions (water deficit stress or drought), the use of tolerant rootstocks leads to an improvement in stomata regulation capacity (stomata closure) [54]. Therefore, stomatal conductance is a useful indicator to determine the ability of plants to adjust gas exchange under water deficit conditions [67]. This regulation is a plant's own response to moisture loss from the substrate and serves to better control water loss by transpiration (F [68].

Another resistance response is through the biosynthesis of organic osmolytes. For example, the lower proline biosynthesis observed in plants grafted on *D. stramonium* demonstrates that the rootstock allows maintaining cellular homeostasis when water availability is reduced and, therefore, has better tolerance to water stress [69]. Plants exposed to stress have developed mechanisms to counteract its effects and ensure their survival, including the accumulation of osmolytes such as mannitol, galactinol, trehalose and proline. These

Table 5
Effect of interaction of water regimes and rootstocks on tomato fruit quality.

Parameters	Rootstock (R)	Irrigation amount (I)				Analysis of Variance			Coefficient of variation (%)
		100% *ETc*	75% *ETc*	50% *ETc*	25% *ETc*	R	I	R × I	
Total Soluble Solids (°Brix)	*S. licopersicum* (self-graft)	6.11 ± 0.60 f	7.11 ± 0.91 e	11.01 ± 0.65 c	15.16 ± 0.41 a	***	***	***	7.24
	D. stramonium	5.92 ± 0.43 f	6.30 ± 0.46 f	10.96 ± 0.47 c	13.89 ± 0.43 b				
	C. betacea	4.40 ± 0.30 g	4.77 ± 0.62 g	6.15 ± 0.64 f	8.18 ± 0.51 d				
	S. quitoens	3.98 ± 0.48 g	6.21 ± 0.48 f	8.00 ± 0.90 d	10.66 ± 0.42 c				
	S. sisymbriifolium	4.96 ± 0.82 g	5.78 ± 0.27 f	8.16 ± 0.58 d	11.32 ± 0.61 c				
Fruit pH	*S. licopersicum* (self-graft)	4.64 ± 0.11 a	4.40 ± 0.11 b	4.14 ± 0.22c	4.01 ± 0.18 d	***	***	**	3.64
	D. stramonium	4.69 ± 0.06 a	4.49 ± 0.10 a	4.44 ± 0.07 b	3.89 ± 0.11 d				
	C. betacea	4.56 ± 0.08 a	4.51 ± 0.13 a	4.30 ± 0.07 b	4.17 ± 0.02 c				
	S. quitoens	4.22 ± 0.08 c	4.15 ± 0.31 c	4.03 ± 0.23 d	3.58 ± 0.36 e				
	S. sisymbriifolium	4.34 ± 0.04 b	4.21 ± 0.07 c	4.06 ± 0.03 d	3.93 ± 0.15 d				
Fruit firmness (N)	*S. licopersicum* (self-graft)	23.19 ± 0.57 f	28.52 ± 4.68 e	32.85 ± 0.44 c	38.96 ± 1.57 a	***	***	***	4.81
	D. stramonium	24.84 ± 1.01 f	26.60 ± 1.19 e	31.18 ± 0.88 d	34.25 ± 0.50 b				
	C. betacea	21.89 ± 1.36 g	24.15 ± 0.66 f	24.46 ± 0.58 f	26.84 ± 0.64 e				
	S. quitoens	23.96 ± 0.47 f	25.66 ± 0.73 f	27.11 ± 0.53 e	27.90 ± 0.92 e				
	S. sisymbriifolium	27.52 ± 0.76 e	28.00 ± 0.48 e	31.04 ± 1.38 d	35.63 ± 0.92 b				
Titratable acidity (%)	*S. licopersicum* (self-graft)	0.27 ± 0.02 f	0.33 ± 0.01 d	0.41 ± 0.01 c	0.49 ± 0.03 b	***	***	***	6.37
	D. stramonium	0.23 ± 0.02 g	0.30 ± 0.01 e	0.39 ± 0.02 c	0.48 ± 0.02 b				
	C. betacea	0.18 ± 0.02 h	0.21 ± 0.01 g	0.26 ± 0.01 f	0.31 ± 0.01 e				
	S. quitoens	0.19 ± 0.01 h	0.21 ± 0.01 g	0.30 ± 0.02 e	0.38 ± 0.02 c				
	S. sisymbriifolium	0.18 ± 0.03 h	0.27 ± 0.02 f	0.33 ± 0.02 d	0.52 ± 0.03 a				
Brix/titratable acidity ratio	*S. licopersicum* (self-graft)	22.99 ± 2.82 b	21.78 ± 3.70 b	26.80 ± 1.31 a	31.05 ± 2.72 a	*	***	***	11.49
	D. stramonium	26.00 ± 3.53 a	21.29 ± 1.61 b	28.01 ± 1.68 a	29.13 ± 1.22 a				
	C. betacea	24.15 ± 2.70 b	22.44 ± 3.57 b	24.11 ± 3.21 b	26.51 ± 2.41 a				
	S. quitoens	20.79 ± 2.62 b	29.20 ± 3.23 a	26.48 ± 4.07 a	27.82 ± 1.58 a				
	S. sisymbriifolium	27.98 ± 6.42 a	21.33 ± 1.35 b	24.87 ± 1.13 b	21.92 ± 1.18 b				
Phenolic content	*S. licopersicum* (self-graft)	28.74 ± 1.49 c	24.89 ± 0.91 d	22.33 ± 2.55 e	21.88 ± 1.09 e	***	***	***	9.2
	D. stramonium	27.21 ± 1.45 c	27.97 ± 1.93 c	20.35 ± 2.26 e	16.05 ± 0.54 f				
	C. betacea	38.03 ± 1.14 a	30.54 ± 2.32 c	23.17 ± 1.35 e	15.09 ± 0.78 f				
	S. quitoens	33.03 ± 4.51 b	17.92 ± 2.41 f	16.41 ± 1.09 f	9.11 ± 0.42 g				
	S. sisymbriifolium	29.75 ± 3.46 c	29.78 ± 4.70 c	27.41 ± 1.69 c	16.52 ± 0.62 f				

Values (±SD) not followed by same letter denote significant differences between treatments (DGC test at $p \leq 0.05$). Significance levels *, **, *** correspond to $p \leq 0.05$, 0.01 and 0.001, respectively.

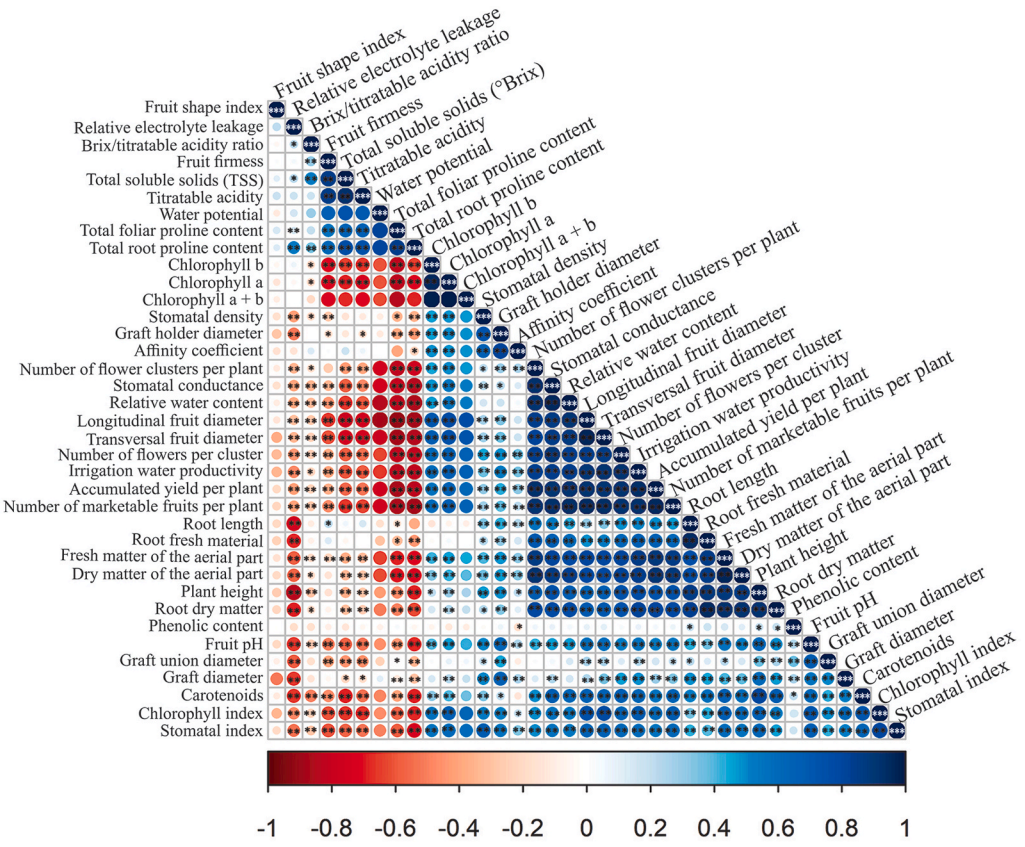

Fig. 3. Pearson correlation coefficient (PCC) heat map matrix, with significance levels expressed with asterisks (*, **, *** correspond to $p \leq 0.05$, 0.01 and 0.001, respectively). Positive correlations are shown in blue and negative correlations in red, according to the scale bar at the bottom. The size of the circle is proportional to the correlation coefficients. The CCPs of the diagonal were 1.

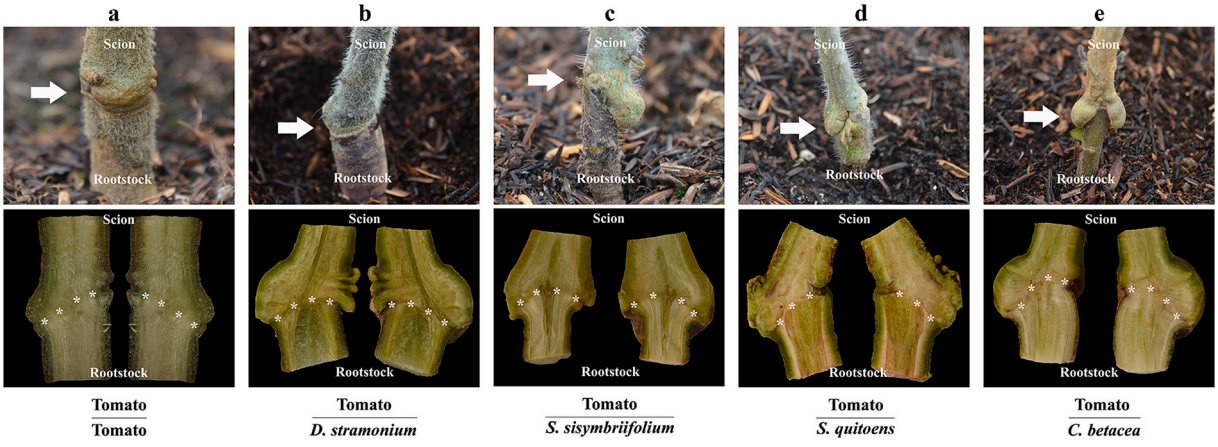

Fig. 4. Field performance and internal characterization of graft union of tomato cv. 'Rambo F1' grafted on five Solanaceae species; (a) *S. licopersicum* (self-graft); (b) *D. stramonium*; (c) *S. sisymbriifolium*; (d) *S. quitoens*; (e) *C. betacea*. Graft interface indicated by asterisks.

osmolytes, during a state of water stress, stabilize proteins and cell membranes, reducing the osmotic potential and preventing cellular dehydration [70,71]. Proline, in particular, has been implicated in multiple roles in plant stress tolerance, serving as a biochemical marker to identify drought-tolerant rootstocks [72]. That is, both osmotic and stomatal adjustments consist of a decrease in water potential in the tissue, which causes water to enter and, therefore, does not decrease turgor or photosynthetic productivity [73]. It should be noted that, for plants with a water potential lower than −0.5 MPa, water potential and water status reveal a more balanced

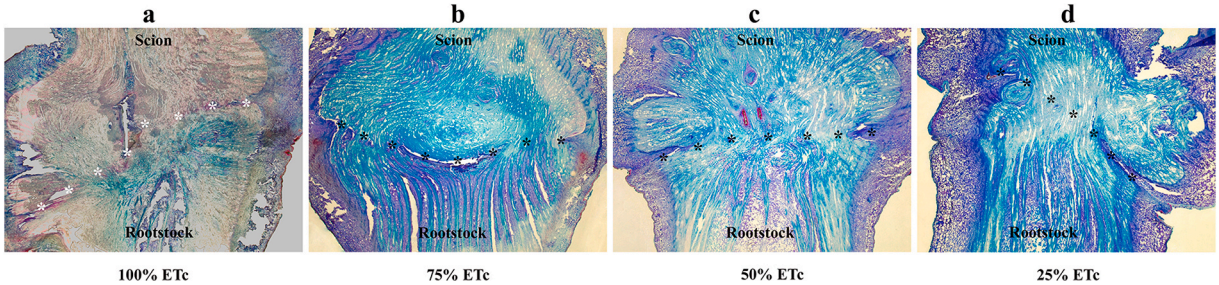

Fig. 5. Anatomical analysis of the tomato/D. stramonium graft according to the amount of irrigation; (a) 100% ETc; (b) 75% ETc; (c) 50% ETc; (d) 25% ETc. Graft interface indicated by asterisks.

relationship during transpiration and water absorption [74].

At the production level, it has been established that the use of tolerant rootstocks can alleviate the adverse effects of stress by optimizing the plant's use of water and nutrients, improving and increasing yield stability rather than simply ensuring plant survival [75]. However, in recent years, fruit and vegetable quality has taken precedence over yield because of its relationship to human nutrition. Although, both productivity and quality of grafted vegetables may differ and be contradictory from the perspective of the grower and the consumer. Vegetable quality is defined primarily by characteristics such as texture, flavor (volatile aromas, acids, sugar) and the content of compounds that promote health (phenols, carotenoids, vitamins, minerals) or are harmful to health (nitrates, heavy metals and pesticides), all of which can be affected by the rootstock as a result of translocation of metabolites [76,77]. On the other hand, consumer demand determines the economic value and represents an essential aspect in the production of grafted vegetables [76]. [78]; concluded that abiotic stress improves certain quality attributes of harvested fruit, in selected wild selected rootstocks, which evidences an alternative to mitigate its undesirable impact. For example, [79]; found that eggplant fruits obtained from plants grafted on *S. sisymbriifolium* had a less intense sour taste and fewer seeds. In the present study, the rootstocks that provided the best traits in terms of °Brix, titratable acidity, pH, firmness, total phenolic content, fruit length and diameter, and yield were *D. stramonium* and *S. sisymbriifolium*, under the different irrigation treatments.

5. Conclusion

This study determined that *Datura stramonium* has a high potential as a tomato rootstock due to its high level of scion compatibility. In addition, *D. stramonium* rootstock had a significant positive impact on morphological, physiological, biochemical, and productive parameters. It allowed a better osmoregulation (induced by a higher relative water content) of the scion, in addition to maintaining a high-water potential and a better photosynthetic efficiency of the tomato, making it more tolerant to water stress. The overall tolerance of the scion resulted in a better yield with a higher number of commercially valuable fruits. The *D. stramonium* rootstock is presented as a species with potential for establishing tomato production areas in scenarios of water scarcity or deficit irrigation cultivation.

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Declaration of competing interest

The authors have no conflict of interest to report.

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.heliyon.2022.e12755.

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