Scientia Horticulturae 282 (2021) 110050

Contents lists available at ScienceDirect

Scientia Horticulturae

journal homepage: www.elsevier.com/locate/scihorti

Grafting of tomato (*Solanum lycopersicum* L.) onto potato (*Solanum tuberosum* L.) to improve salinity tolerance

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ARTICLE INFO

Keywords:
Grafting
Dry mass
Physiology
Root and salinity

ABSTRACT

Grafting with different rootstocks may provide increased tolerance and yield, even under poor-quality irrigation conditions. We examined the effects of potato rootstock on physiology, dry mass, and yield of tomato scion in pots irrigated with saline water. Tomato (cv. Ikram), potato (cv. Charlotte) and grafted (cv. Ikram/Charlotte) plants were subjected to saline and non-saline water-irrigation treatments (electrical conductivity 5.0 and 1.0 dS m^{-1}, respectively). Physiological, mineral, dry mass and yield analyses were performed. Potato rootstock unchanged the total plant dry mass without disturbing the physiology of the tomato scion under saline water irrigation. The grafted plants showed differential root trait responses with balanced mineral partitioning across plant parts under saline water irrigation. Grafted plants were superior in water productivity by 56.8 and 70.5 % over the control plants under saline and non-saline water-irrigations, respectively. Potato rootstock could improve the tolerance of tomato scion to saline water irrigation through distinct changes in dry mass allocation, and the induction of mineral-compartmentalization processes. The results of this study suggest that the use of potato rootstock may be a good strategy for increasing tolerance to saline water irrigation, as well as the production of both fruits and tubers in a single plant.

1. Introduction

Global supply of good-quality water for irrigation has become limited due to intense competition from urban, industrial, and recreational users. This has promoted the use of alternative water sources, such as treated effluent and saline ground water, which contain relatively high levels of soluble salts. Indiscriminate use of poor-quality water for irrigation hampers soil productivity through salinity. More than 50 % of irrigated arid and semiarid lands have been shown to be affected by salinity (Rozema and Flowers, 2008) that is strictly associated with irrigation water containing high salt concentrations (Tanji and Kielen, 2002). Saline water irrigation has an adverse effect on soil–water–plant relations, often resulting in negative effects on crop physiology and productive capacity (Plaut et al., 2013). It may induce Na^+ and Cl^- accumulation in plants, causing osmotic stress and ion imbalances in cells (Tavakkoli et al., 2010), interference with photosynthetic metabolism, and interrupted nutrient uptake (Rodrigues et al., 2014). Thus, there is an urgent need to develop vegetable crops that are productive under saline conditions, but using traditional, molecular breeding and genetic engineering approaches takes considerable time, and is genetically and physiologically complex (Ashraf and Foolad, 2007).

Grafting is a promising technique, regarded as a rapid and economical solution (Genova et al., 2013) to improving stress tolerance in solanaceous vegetables (Colla et al., 2010; Flores et al., 2010). In a successful graft, the aboveground part (scion) is used to produce high nutritious yield while the belowground part (rootstock) is used to tolerate soil borne stresses. The enhanced use of grafted tomato has gained popularity worldwide (Lee et al., 2010) for high yield, quality, and tolerance to biotic (Barrett et al., 2012) and abiotic stresses (King et al., 2010; Savvas et al., 2010). Experiments have confirmed that grafting tomato provides an alternative way to increase yield under saline conditions (Estan et al., 2005; Santa-Cruz et al., 2002).

Wild tomato rootstocks are commonly used for grafting of tomatoes. Such rootstocks have been shown to limit the transport of Na^+ and Cl^- to the shoot, thereby conferring salt tolerance (Estan et al., 2005). However, the rootstock's efficiency in reducing toxic salt depends on the

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https://doi.org/10.1016/j.scienta.2021.110050
Received 21 November 2020; Received in revised form 7 February 2021; Accepted 13 February 2021
Available online 26 February 2021

ion-exclusion ability of the graft combination (Martínez-Rodríguez et al., 2008). Grafting negates the stress effects of salinity by maintaining a low Na^+ and a high K^+/Na^+ ratio in the shoot, and improving leaf stomatal conductance (Wang et al., 2017), though these grafts improve tolerance to a single stress for only a short period and not strongly (Venema et al., 2008).

Rootstocks of different species may influence tolerance through their interactive combinations with the scion (Kawaguchi et al., 2008). These can be used to expand the rootstock diversity for strong tolerance to future environmental pressures. Solanaceous crops such as eggplant and potato have been grafted for the cultivation of tomato to cope with various stresses. Grafting eggplant (*Solanum* melongena) on tomato (*Solanum* lycopersicum) rootstock enhanced verticillium wilt tolerance (Liu et al., 2009), and eggplant rootstock grafted to tomatoes displayed tolerance to flooding and waterlogging, as well as resistance to soil borne diseases (King et al., 2010). Wild Solanaceae rootstocks, such as common purple eggplant (*Solanum melongena*), *Solanum habrochaites* and other species, provide broadened tolerance, as well as a large range of fruit colors and shapes (Keatinge et al., 2014).

Grafting of tomato on potato rootstock has been reported by Arefin et al. (2019); Bünemann and Grassia (1973); Kelly and Somers (1948); Kumar (2011); Peres et al. (2005); Su-e et al. (2010), and Tsror and Nachmias (1995). Kelly and Somers (1948) reported that tuber yield and quality of the interspecific (tomato/potato) graft was regulated by the potato genome. The inverse graft combination (potato/tomato) expressed graft-transmissible RNA that could alter the scion phenotype (Kudo and Harada, 2007). This could therefore create a novel system for cultivar improvement in vegetable crops.

Several attempts have been made to address the effects of using tomato as both scion and rootstock on salinity-stress tolerance (Estan et al., 2005; Santa-Cruz et al., 2002; Martínez-Rodríguez et al., 2008). However, to the best of our knowledge, no information is available regarding the responses of tomato scion grafted on potato rootstock to saline water irrigation. Furthermore, a complete analysis of Na, K, Ca and Mg partitioning within the graft (tomato/potato) system is necessary to better understand rootstock–scion interactions under saline water irrigation (Rouphael et al., 2010). With this in mind, we aimed to identify the physiological responses and mineral ion distribution under saline water irrigation that are responsible for the salinity tolerance of the graft, and to evaluate the grafts in terms of dry mass, yield and fruit quality and water productivity. In this study, the role of root traits in altering the salinity-stress perception of the shoots is given special attention. We hypothesized that grafting of tomato on potato (*Solanum lycopersicum/Solanum tuberosum*) would improve tomato's salinity tolerance and yield through changes in the root and shoot traits.

2. Materials and methods

2.1. Plant material and growth conditions

A grafting experiment was conducted in a controlled greenhouse at the Sede Boqer Campus (30°52′ 08.04″ N and 34°47′ 33″ E) of Ben-Gurion University of the Negev, Israel, from 2016 to 2017. The growth conditions inside the greenhouse were as follows: max/min temperature 24/20 °C day/night (Supplemental Fig. 1 in Online Resource), respectively, mean relative humidity 80 %, and photosynthetic photon flux density (PPFD) 800 μmol m^{-2} s^{-1} (photoperiod, 14 h). Seedlings of tomato (*Solanum lycopersicum* L. var. Ikram) were supplied by the Syngenta Company (Zeraim Gedera, Kibbutz Revadim, Israel) and used as the scion, and potato (*Solanum tuberosum* L. var. Charlotte) was used as the rootstock. The potato tubers were treated with a gibberellic acid solution (10 mg mL^{-1}) for 15 min to break dormancy. Tomato seedlings and potato seed tubers were planted on 1st June 2017 in pots (20-L capacity, 450 mm in height, 390 mm in diameter) filled with sandy loam soil (30 kg pot^{-1}) consisting of 51.4 % silt, 8.8 % clay and 39.8 % sand.

2.2. Grafting

Grafting of tomato and potato was carried out 30 days after dormancy-breaking and pictorially described in Supplemental Fig. 2. The tomato scions were prepared by cutting the stem with a razor blade below the second or third leaf from the apex. Potato rootstocks were prepared by cutting transversely 10 cm above the soil level with a razor blade. The scion was cut into a wedge shape and inserted into a "V"-shaped incision in the stock. Grafts were tied with grafting tape to ensure the scion–rootstock connection. Grafted plants (cv. Ikram/Charlotte) were covered with transparent plastic to provide a humid environment. After seven days, the cover was removed, and the plants were acclimatized in the greenhouse. The plants were fertilized with a solution of NPK 20−20-20 plus micronutrients at a concentration of 1.0 g L^{-1}.

2.3. Experimental treatments and design

In the greenhouse, the tomato, grafted (cv. Ikram/Charlotte) and potato plants were arranged in a completely randomized design (CRD) with six replications. In each repetition, one plant per pot was maintained and supplied with saline or non-saline irrigation treatments. All the pots were placed on benches at 2 m distance between the plants to avoid competitive effects. The saline water was prepared in 500-L containers by mixing NaCl and $CaCl_2$ salts with 500 g of fertilizer (Poly-feed GG, NPK 20−20-20 at a concentration of 1.0 g L^{-1}), giving a final electrical conductivity (EC) of 5.0 dS m^{-1}. A similar quantity of non-saline solution was prepared without chloride salts, giving a final EC of 1.0 dS m^{-1}. Fertigation was applied through a drip irrigation system (2.0-L discharge drippers, Netafim Irrigation, Israel) starting from 20 days after grafting (DAG) until the end of the experiment. Irrigation, evapotranspiration and leaching fraction were monitored during the experiment, and are given in Supplemental Fig. 3 in Online Resource. The electrical conductivity of drainage water from the pots were measured and given in Supplemental Table 1. The grafted plants were maintained without flowers up to 45 DAG, since these could represent a competing sink for the potato tubers (Peres et al., 2005). Tuberization was evaluated at 80 DAG.

2.4. Leaf physiology

Photosynthetic rate and stomatal conductance were measured with a portable photosynthesis system (LI-6400XT; LI−COR, Lincoln, NE, USA). Briefly, green leaves were enclosed in the portable photosynthesis system under a light intensity of 800 μmol m^{-2} s^{-1} PPFD and 400 μmol mol^{-1} CO_2 at 25 °C leaf temperature and relative humidity between 40 and 55 %. Non-photochemical quenching (NPQ) and electron-transport rate (ETR) were measured by a Mini-PAM (Walz, Effeltrich, Germany) with a leaf clip holder (Model 2030-B). All physiological parameters were measured on the third leaf from the plant apex at the same time (1200–1400 h) of day (65 DAG) to remove circadian effects. Leaf samples were frozen (-20 °C) overnight and then squeezed to extract sap (10 μL) for measuring leaf osmolality (mmol kg^{-1}) with a vapor pressure osmometer (Vapro model 5520, Wescor Inc., Logan, UT, USA).

2.5. Yield and yield components

Tomato fruit were harvested at 120 and 135 DAG. Fruits were picked manually, and the total yield and average fruit mass were evaluated. Fruit total soluble solids (TSS) was measured in tomato juice samples with a refractometer and expressed as °Brix (Pregnolatto and Pregnolatto, 1985). Tubers were harvested from the grafted and potato plants and analyzed for yield, average tuber mass, and total number at 135 DAG.

Total plant dry mass was measured at 135 DAG using a precision weighing balance (EI-i series, A&D Company Limited, Japan) by the sum of the individual dry masses of leaf, stem, root, fruit and tuber. In this

study, we used term water productivity as the measure of yield gain (fruits and tubers) from the use of unit of water consumed in the grafted plant and expressed as Kg m^{-3}.

2.6. Root morphology

At the end of the experiment (135 DAG), the root morphology (average root diameter, root volume and root density) of tomato, grafts (cv. Ikram/Charlotte) and potato were investigated in response to the saline water irrigation. The entire root system was scanned (depth-wise) using the Epson Expression 10000XL with a transparency unit and analyzed by WINRHIZO PRO 2005 Software (Regent Instruments Inc., Ville de Québec, Canada).

2.7. Mineral partitioning analysis

At the end of the experiment, samples of roots, stems, leaves, fruits and tubers were collected for mineral analyses. Specifically, 2.5 mg of the dried (65 °C, for 72 h), finely ground (through an IKA mill, Labortechnik, Staufen, Germany) samples was digested with nitric acid, and the filtered samples were used for mineral analysis. Cations (Na, K, Ca, and Mg) were analyzed using inductively coupled plasma-optical emission spectroscopy (ICP-OES, Optima 5300 V) with 2 % precision. The ratios of K/Na, Ca/Na, and Mg/Na were calculated from the concentrations of K, Ca, Mg and Na ions.

2.8. Statistical analysis

The collected data were statistically processed. Analysis of variance (ANOVA) was performed referring to $P < 0.05$ and using JMP 2007 (SAS Institute, Cary, NC, USA) to evaluate the effects of plant type (tomato, graft and potato) under saline and non-saline water irrigation. The means were separated by Tukey's honest significant difference (Tukey HSD) at $P < 0.05$ on the planned variables.

3. Results

3.1. Grafting of tomato onto potato alters the total dry mass distributions

The total dry mass of a single plant (Fig. 1a) was obtained from the sum of the individual plant organs (root, tuber, stem, leaf and fruit) (Supplemental Table 2 in Online Resource). No differences were found in leaf and stem dry masses of the grafted and tomato plants between non-saline and saline water irrigation treatments. Moreover, saline water irrigation did not affect the total dry mass of the tomato or grafted plants, but decreased it significantly in potato (Fig. 1a; $P < 0.05$). No significant change in total dry mass was observed in grafted plants under either irrigation treatment compared to non-saline water irrigated tomatoes. Comparing irrigation with non-saline vs. saline water, the leaf and fruit dry mass allocations (Fig. 1b) for the grafted and tomato plants were unchanged, but stem dry mass distribution was reduced under saline water irrigation. In the grafted plants, this alteration was due to unaffected tuber dry mass distribution even under saline water irrigation (Fig. 1b). Saline water irrigation decreased the allocation of root dry mass in tomato and increase in potato, but did not affect in grafted plants (Fig. 1b).

3.2. Variation in root traits caused by salinity and grafting

In comparison to non-saline water irrigation, the root volume of the grafted plant was significantly affected by saline water irrigation which did not show significant effects on average root diameter, root length density and root mass density (Supplemental Fig. 4 & 5 in Online Resource). The root length density of the grafted plants was significantly ($P < 0.05$) higher, by 72.6 %, under saline water irrigation than that of potato. Conversely, these plants presented similar root mass density and diameter values under saline water irrigation (Supplemental Fig. 4 & 5 in Online Resource).

The root length density of the grafted plants declined significantly ($P < 0.05$), by 47.3 %, at 0–15 cm soil depth under saline water irrigation (Fig. 2). Similar irrigation did not affect the root length density or mean diameter of the grafted plants at 15–30 cm soil depth.

At 0–45 cm soil depth, the root diameter and volume of the potato and grafted plants were not affected by saline water irrigation (Fig. 3). In comparison to potato, the grafted plants had significantly higher root length density, by 76.0 % and 79.2 % at 15–30 cm and 30−45 cm soil depth, respectively.

3.3. Potato rootstock alters the physiology of tomato leaves

The leaf gas-exchange results indicated that saline water irrigation significantly affected leaf photosynthetic rate and stomatal conductance (Table 1) in tomato and grafted plants. However, the leaf gas exchange values did not differ between the grafted plant and non-grafted tomato

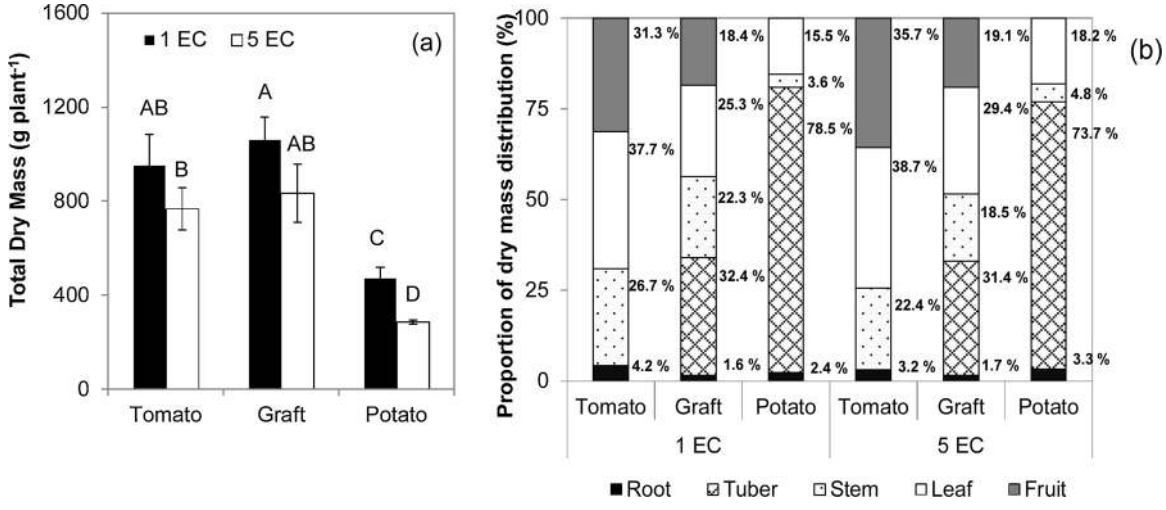

Fig. 1. Total dry mass of tomato, grafted and potato plants under non-saline (1 EC: Electrical Conductivity 1.0 dS/m) and saline (5 EC: Electrical Conductivity 5.0 dS/m) irrigation (a), at 135 days after grafting. Proportional dry mass distribution (%) between plant parts (root, tuber, stem, leaf and fruit) under saline irrigation (b). Actual dry mass allocation is provided in Supplemental Table 1 in Online Resource. Different letters indicate significant difference among graft treatments under non-saline and saline water irrigations ($P < 0.05$). Each column represents the average ± SE of six plants per treatment.

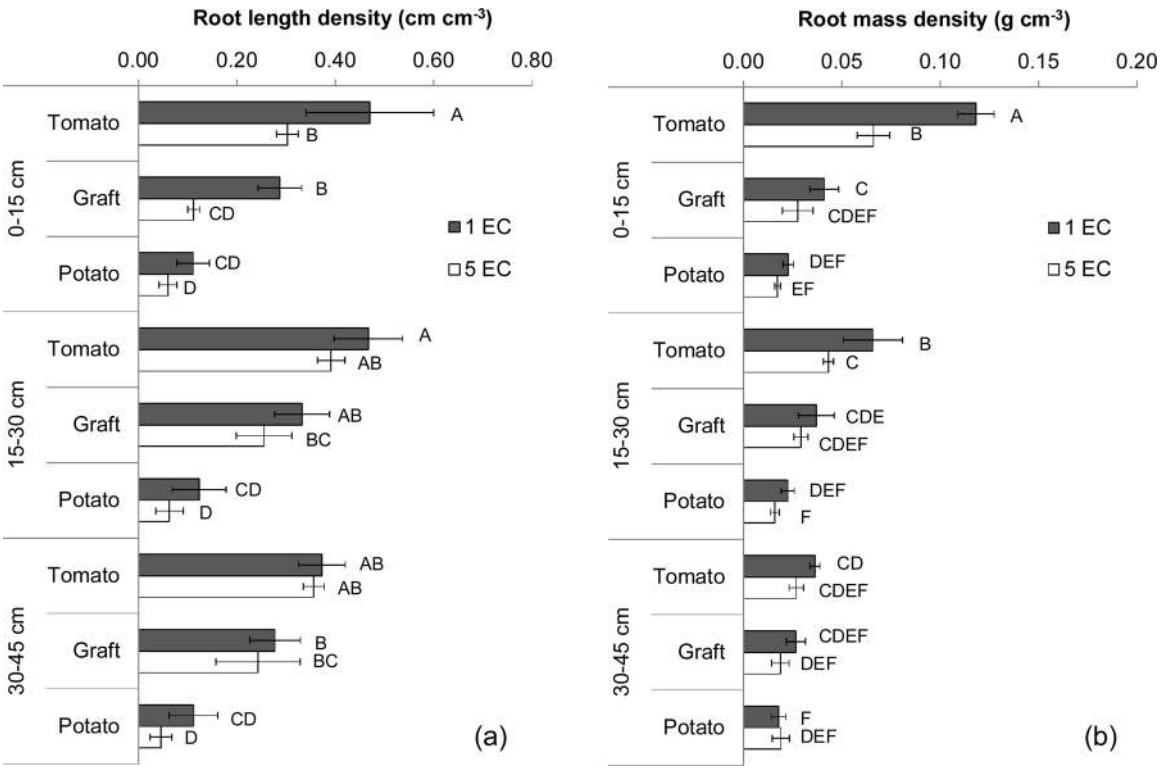

Fig. 2. Variation in root traits of tomato, grafted and potato plants under non-saline (1 EC) and saline (5 EC) irrigation. Effect of graft under saline irrigation 135 days after grafting on (a) root length density and (b) root mass density at different soil depths (0–15, 15–30 and 30–45 cm). The average root length density and root mass density at entire soil depth (0-45 cm) given in supplemental Fig. 5 in online resources. Different letters indicate significant difference among graft treatments under non-saline and saline water irrigations ($P < 0.05$). Each column represents the average ± SE of six plants per treatment.

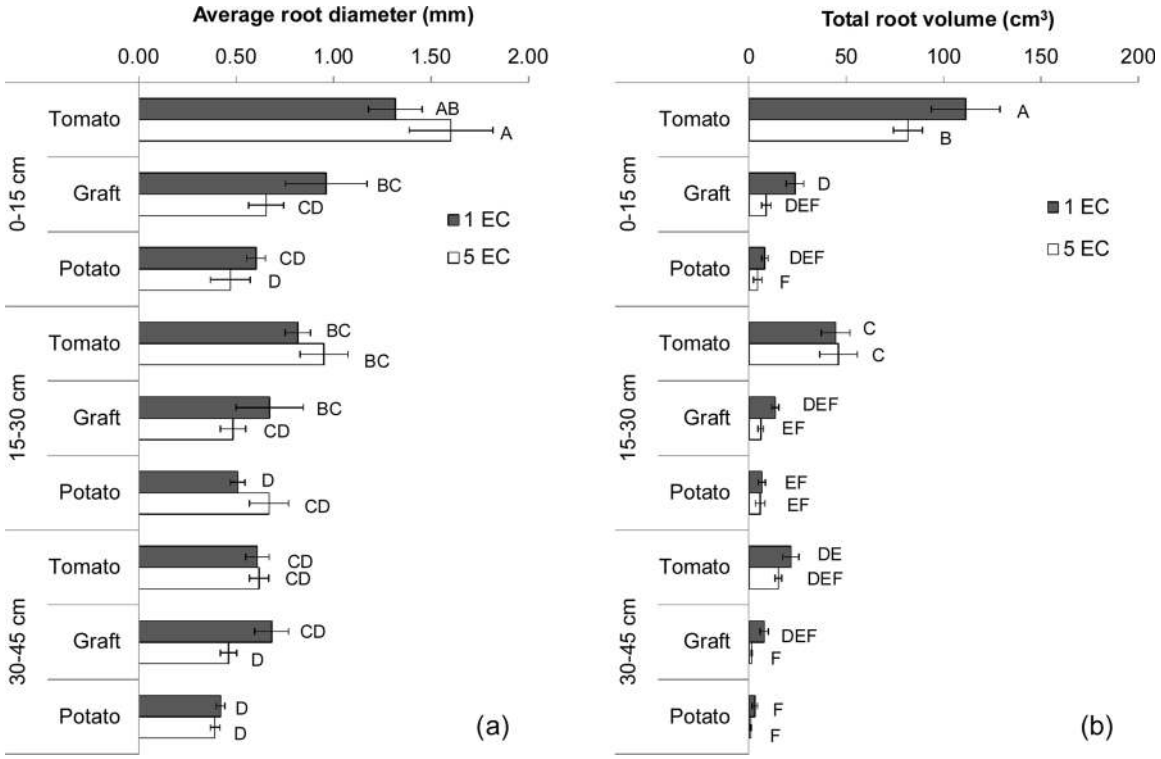

Fig. 3. Variation in root traits of tomato, grafted and potato plants under non-saline (1 EC) and saline (5 EC) irrigation. Effect of graft under saline irrigation 135 days after grafting on (a) average root diameter and (b) root volume at different soil depths (0–15, 15–30 and 30–45 cm). The average root diameter and total root volume at entire soil depth (0-45 cm) given in supplemental Fig. 4 in online resources. Different letters indicate significant difference among graft treatments under non-saline and saline water irrigations ($P < 0.05$). Each column represents the average ± SE of six plants per treatment.

Table 1
Performance of tomato and grafted plants under non-saline (1 EC) and saline (5 EC) irrigation in terms of photosynthetic rate, stomatal conductance, electron-transport rate, non-photochemical quenching and leaf osmolality.

Irrigation	Plant type	Photosynthetic rate (μmol m^{-2} s^{-1})	Stomatal conductance (mmol m^{-2} s^{-1})	Electron-transport rate (μM m^{-2} s^{-1})	Non-photochemical quenching (-)	Leaf osmolality (mmol kg^{-1})
1 EC	Tomato	20.8 ± 0.8^{A}	298.2 ± 19.5^{AB}	53.6 ± 2.8	1.44 ± 0.03	271.2 ± 34.6^{C}
	Graft	22.1 ± 1.0^{A}	310.8 ± 13.2^{A}	47.4 ± 1.2	1.55 ± 0.12	470.5 ± 22.2^{B}
5 EC	Tomato	14.7 ± 0.6^{B}	158.2 ± 29.4^{C}	47.1 ± 4.1	1.57 ± 0.12	713.2 ± 37.0^{A}
	Graft	16.5 ± 1.0^{B}	198.3 ± 34.0^{BC}	45.6 ± 2.5	1.62 ± 0.18	762.8 ± 22.2^{A}
				n.s.	n.s.	

Different letters indicate significant difference between treatments ($P < 0.05$). Each value represents the average ± SE of six plants per treatment. n.s.: non-significant.

plants under either of saline and non-saline water irrigation. The electron transport rate (ETR) and non-photochemical quenching (NPQ) of tomato and grafted plants were not affected by the type of water irrigation (Table 1). Saline water irrigation significantly increased leaf osmolality in grafted and tomato plants (compared to non-saline water irrigation). Under non-saline water irrigation, the grafted plants had significantly higher leaf osmolality (by 42.4 %; $P < 0.05$) than the tomato plants (Table 1).

3.4. Potato rootstock and tomato scion balances partitioning of mineral ions

The leaf and fruit Na concentrations were significantly lower in the grafted plants, by 54.2 % and 66.2 %, compared to their counterparts in the tomato plants under saline water irrigation (Table 2). Under non-saline water irrigation, the grafted plants showed a significant reduction in fruit and leaf Na concentration, whereas the stem Na concentration was not different from that of tomato. Root and tuber Na concentration of grafted plants showed no variation (Table 2) under saline water irrigation, when compared to that of potato.

K concentration was significantly reduced by saline water irrigation in the fruit of tomato and grafted plants compared to non-saline water irrigation and grafting changed the K concentrations in fruit and leaves under saline and non-saline water irrigation, compared to their counterparts in tomato plants. The Ca and Mg concentrations did not vary in the stems or roots of tomato or grafted plants, but significantly increased in the fruit (59.0 % and 43.1 %, respectively; $P < 0.05$) of the grafted vs. tomato plants under saline water irrigation. Similar increase in fruit Ca and Mg concentration was noted in the grafted plants (35.4 % and 25.3 %, respectively over the tomato; $P < 0.05$) under non-saline irrigation. Mg concentration accumulated significantly more in the grafted plants' leaves (48.8 %) and tubers (42.8 %) than in the leaves of tomato and tubers of potato ($P < 0.05$).

The grafted plants displayed higher K/Na and Mg/Na ratios in the leaves, stem and fruit as compared to tomato under non-saline water irrigation (Table 2). Under saline water irrigation, the grafted plants' fruit and leaves showed significantly higher ratios of K/Na (81.5 % and 68.1 %, respectively), Ca/Na (86.5 % and 64.4 %, respectively) and Mg/Na (78.3 % and 66.6 %, respectively) than in tomato plants. The supply of $CaCl_2$ and NaCl contributed by the saline water irrigation caused no variation in Ca concentration or Ca/Na ratio in the roots. The grafted plants had a higher ($P < 0.05$) Ca/Na ratio (3.7) in their fruit, as evidenced by the absence of blossom end rot (data not shown) under saline water irrigation, whereas this disorder appeared in the fruit of tomato which had a low Ca/Na ratio (0.5).

3.5. Yield and water productivity response of tomato was modulated by potato rootstock

The total fruit yield and average fruit mass per fruit of grafted plants were unaffected under non-saline water irrigation, whereas they were significantly decreased under saline water irrigation (Fig. 4a,b). The fruit yield and average fruit mass of grafted plants were not different from tomato plants under saline water irrigation (Fig. 4a), whereas grafted plants achieved 78.9 % fruit yield of tomatoes under the non-saline water irrigation. Under the saline water irrigation, the fruit TSS

Table 2
Effects of grafting under non-saline (1 EC) and saline (5 EC) irrigation on distribution of K^{+}, Ca^{2+}, Mg^{2+} and Na^{+} concentrations, and K/Na, Ca/Na and Mg/Na ratios in the different parts (fruit, leaf, stem, tuber and root) of tomato, grafted and potato plants.

Plant organ	Irrigation	Plant type	K (mg/g of DW)	Ca (mg/g of DW)	Mg (mg/g of DW)	Na (mg/g of DW)	K/Na ratio	Ca/Na ratio	Mg/Na ratio
Fruit	1 EC	Tomato	10.7 ± 0.7^{B}	11.6 ± 0.7^{B}	6.7 ± 0.5^{B}	1.6 ± 0.1^{C}	6.8 ± 0.57^{B}	7.4 ± 0.73^{B}	4.3 ± 0.42^{B}
		Graft	14.3 ± 0.6^{A}	15.7 ± 1.2^{A}	8.4 ± 0.7^{A}	1.0 ± 0.1^{D}	14.7 ± 1.90^{A}	15.9 ± 1.46^{A}	8.5 ± 0.62^{A}
	5 EC	Tomato	4.6 ± 0.3^{D}	3.4 ± 0.6^{D}	2.9 ± 0.1^{D}	6.5 ± 0.3^{A}	0.7 ± 0.06^{D}	0.5 ± 0.11^{D}	0.5 ± 0.00^{D}
		Graft	8.4 ± 0.1^{C}	8.3 ± 0.5^{C}	5.1 ± 0.2^{C}	2.2 ± 0.1^{B}	3.8 ± 0.24^{C}	3.7 ± 0.27^{C}	2.3 ± 0.14^{C}
Leaf	1 EC	Tomato	16.2 ± 0.4^{A}	27.7 ± 1.2^{A}	3.6 ± 0.2^{AB}	1.4 ± 0.1^{C}	11.3 ± 0.6^{B}	19.6 ± 2.3^{B}	2.5 ± 0.1^{B}
		Graft	17.4 ± 3.0^{A}	25.4 ± 2.8^{A}	4.3 ± 0.8^{A}	0.7 ± 0.1^{D}	27.2 ± 2.5^{A}	44.4 ± 13.3^{A}	7.0 ± 1.4^{A}
	5 EC	Tomato	10.4 ± 0.6^{B}	24.4 ± 2.9^{A}	2.3 ± 0.1^{B}	15.5 ± 1.3^{A}	0.7 ± 0.0^{D}	1.6 ± 0.3^{D}	0.2 ± 0.0^{C}
		Graft	15.3 ± 1.2^{A}	31.4 ± 1.5^{A}	4.5 ± 0.2^{A}	7.1 ± 0.4^{B}	2.2 ± 0.2^{C}	4.5 ± 0.5^{C}	0.6 ± 0.0^{B}
Stem	1 EC	Tomato	15.5 ± 3.3^{AB}	7.0 ± 0.4^{A}	1.2 ± 0.2^{A}	1.3 ± 0.1^{B}	12.7 ± 3.6^{B}	5.6 ± 0.6^{B}	0.9 ± 0.3^{B}
		Graft	24.6 ± 5.3^{A}	7.1 ± 0.5^{A}	1.5 ± 0.3^{A}	0.9 ± 0.2^{B}	27.6 ± 3.2^{A}	8.4 ± 1.0^{A}	1.8 ± 0.1^{A}
	5 EC	Tomato	9.6 ± 1.4^{B}	10.4 ± 1.7^{A}	0.9 ± 0.2^{A}	9.1 ± 1.2^{A}	1.1 ± 0.3^{C}	1.2 ± 0.3^{C}	0.1 ± 0.0^{C}
		Graft	17.9 ± 0.1^{AB}	7.9 ± 0.2^{A}	1.4 ± 0.2^{A}	6.0 ± 1.0^{A}	3.1 ± 0.5^{BC}	1.4 ± 0.2^{C}	0.2 ± 0.0^{C}
Tuber	1 EC	Graft	4.6 ± 0.9^{A}	5.5 ± 0.3^{A}	1.1 ± 0.1^{A}	1.2 ± 0.3^{B}	4.0 ± 0.47^{AB}	5.1 ± 1.37^{A}	1.0 ± 0.25^{A}
		Potato	6.4 ± 1.9^{A}	3.9 ± 0.6^{B}	0.5 ± 0.0^{C}	0.9 ± 0.1^{B}	7.8 ± 2.42^{A}	4.9 ± 1.64^{A}	0.6 ± 0.10^{AB}
	5 EC	Graft	7.7 ± 1.7^{A}	1.5 ± 0.3^{C}	0.7 ± 0.0^{B}	4.5 ± 0.6^{A}	1.7 ± 0.37^{B}	0.4 ± 0.11^{B}	0.2 ± 0.03^{BC}
		Potato	7.7 ± 1.0^{A}	1.0 ± 0.2^{C}	0.4 ± 0.0^{C}	3.9 ± 0.8^{A}	2.1 ± 0.22^{B}	0.3 ± 0.09^{B}	0.1 ± 0.01^{C}
Root	1 EC	Graft	7.0 ± 0.2^{A}	33.3 ± 3.5^{A}	11.6 ± 0.8^{A}	2.0 ± 0.1^{B}	3.5 ± 0.2^{A}	16.5 ± 1.2^{A}	5.8 ± 0.6^{A}
		Potato	8.1 ± 0.5^{A}	20.4 ± 3.5^{AB}	10.9 ± 0.7^{A}	2.2 ± 0.2^{B}	3.8 ± 0.2^{A}	9.4 ± 1.1^{B}	5.3 ± 0.8^{A}
	5 EC	Graft	6.6 ± 0.4^{A}	23.8 ± 2.9^{AB}	6.7 ± 0.2^{B}	6.8 ± 0.5^{A}	1.0 ± 0.0^{B}	3.5 ± 0.4^{C}	1.0 ± 0.1^{B}
		Potato	6.8 ± 0.1^{A}	19.1 ± 1.9^{B}	7.0 ± 1.3^{B}	6.5 ± 0.6^{A}	1.1 ± 0.1^{B}	2.9 ± 0.3^{C}	1.1 ± 0.2^{B}

Different letters indicate significant difference between graft treatments under non-saline and saline water irrigations ($P < 0.05$). Each value represents the average ± SE of three plants per treatment.

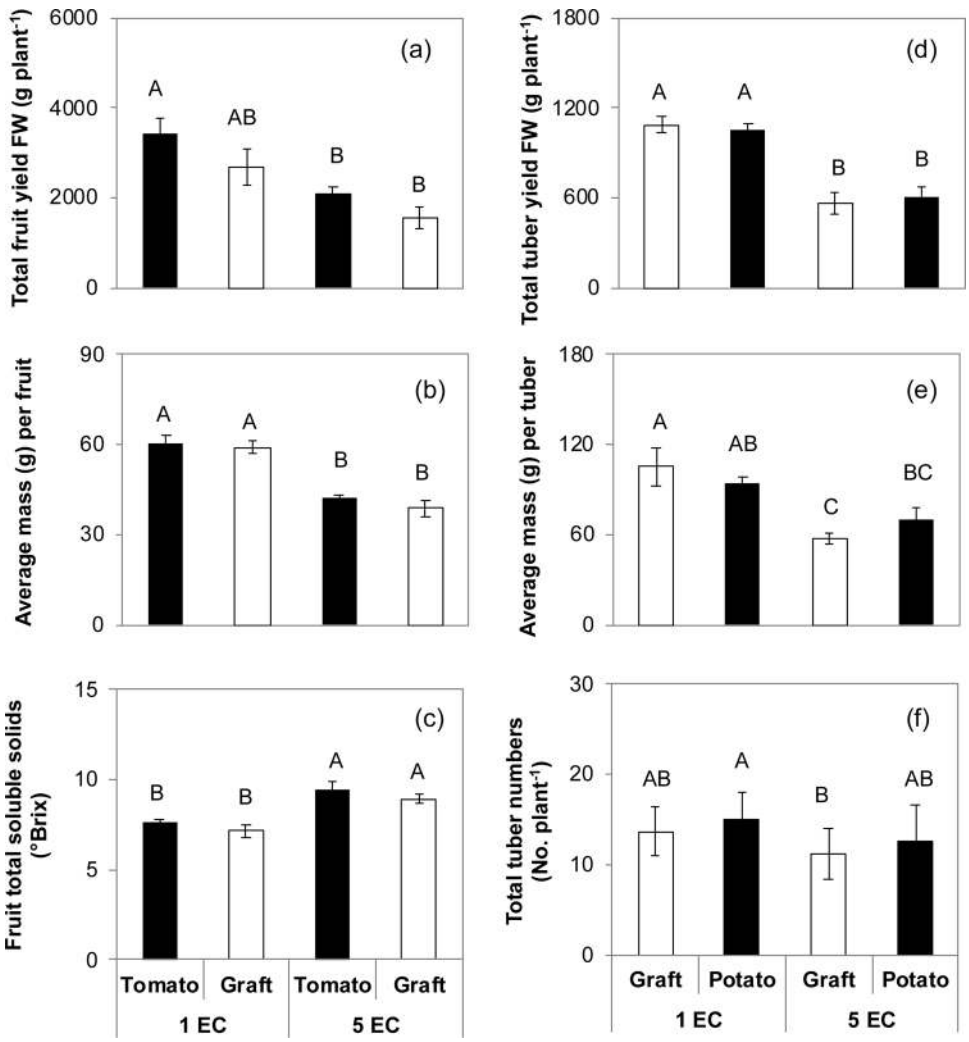

Fig. 4. Yield and yield components of grafted vs. tomato or potato plants under non-saline (1 EC) and saline (5 EC) irrigation. (a) Total fruit yield Fresh Weight, (b) average fruit mass per fruit, (c) fruit total soluble solids (TSS) content, (d) total tuber yield Fresh Weight, (e) average tuber mass per tuber and (f) total tuber number, at 135 days after grafting. Different letters indicate significant difference between graft treatments under non-saline and saline water irrigations ($P < 0.05$). Each column represents the average ± SE of six plants per treatment.

content (Fig. 4c) of grafted (19.6 %) and tomato (19.2 %) plants was significantly higher than that under non-saline water irrigation; however, there was no difference in TSS content between the fruit of the tomato and grafted plants. The total tuber yields (Fig. 4d) of the potato and grafted plants were significantly reduced due to a decrease in the number of tubers (Fig. 4f) per plant (18.2 %) and average tuber dry mass (45.8 %) under saline water irrigation. However, the yield difference between the potato and grafted plants (Fig. 4d) was non-significant under saline water irrigation. The grafted plants produced fruit aboveground (2693 g plant^{-1} and 1559 g plant^{-1}) and tubers belowground (1084 g plant^{-1} and 567 g plant^{-1}) under non-saline and saline water irrigation, respectively.

The water productivity of the grafted plant was higher compared with that of control (by 70.5 % and 56.8 %) under non-saline and saline water irrigation, respectively (Table 3). The water productivity was calculated as the sum of the fresh mass of the potato tubers and the tomato fruits divided by the irrigation water volume. In order to compare between the graft (which produce both tubers and tomato fruits), the volume of water was divided by two for the grafted plants. Additionally, the yield of the control was calculated by summing the mass of the tomato fruits in one plant with the potato tubers of the second plant.

Table 3
Water Productivity of graft vs. control (tomato and potato) plants under non-saline (1 EC) and saline (5 EC) irrigation.

Irrigation	Plant type	Water Productivity (Kg m^{-3})
1 EC	Control	6.1 ± 0.5^{B}
	Graft	10.4 ± 1.2^{A}
5 EC	Control	3.7 ± 0.3^{C}
	Graft	5.8 ± 0.8^{B}

Different letters indicate significant difference between treatments ($P < 0.05$). Each value represents the average ± SE of six plants per treatment.

4. Discussion

We found that the type of irrigation [saline (EC 5.0 dS m^{-1}) or non-saline (EC 1.0 dS m^{-1}) water] had no effect on leaf, stem (Supplemental Table 2 in Online Resource) or total dry masses of tomato and grafted plants (Fig. 1a). Unaffected growth (i.e. shoot and root dry mass) of the grafted plants found better in reducing the consequences of salinity than tomato due to the better grafting combination using the tomato scion onto potato rootstock. This is supported by Ferreira-Silva et al. (2010) and Giuffrida et al. (2014), who found that the dry mass of root system predominates in the compatibility between scion and rootstock. In the present experiment, grafting altered the dry mass partitioning within the plant under non-saline water irrigation (Fig. 1b). Saline water irrigation affected the partitioning of dry mass between vegetative and reproductive organs in potato and tomato plants, whereas the grafted plants showed less altered than under non-saline water irrigation. These results confirm earlier experiments (Estan et al., 2005; Santa-Cruz et al., 2002; He et al., 2009) on the dry mass response of different commercially

grafted tomatoes under saline water irrigation. The tomato scion/potato rootstock combination resulting in unchanged fruit and tuber dry mass under saline water irrigation, as previously observed for an eggplant scion grafted onto a tomato rootstock under salinity (Giuffrida et al., 2014). Physiological interactions between the rootstock and scion genotypes can enhance scion growth and biomass (Colla et al., 2010). The distribution of leaf and root dry mass was not changed in the grafted plant could be a favorable response to saline water irrigation. This was supported by Satti and Lopez (1994) and is thus proposed as the reason for the reduced total dry mass content along with the poor dry mass allocation of potato under saline water irrigation. A greater proportion of photoassimilates are transferred from the stem to the reproductive organs under saline water irrigation (Hamed et al., 2011), resulting in the unaltered tuber dry mass allocation in the grafted plants (Fig. 1b). Under saline water irrigation, the undisturbed leaf physiological activities (Krasensky and Jonak, 2012), the interdependent relationship between scion and rootstock that may ensure a favorable supply of photoassimilates (Orsini et al., 2013), and the balanced dry mass distribution between source (leaf, stem and root) and sink (fruit and tubers) are proposed as the reasons for the unaffected total dry mass of the grafted plants when compared to the tomatoes.

The leaf photosynthetic rates of tomato and grafted plants were sensitive to saline water irrigation (Table 1). Implying the occurrence of non-stomatal limitations; this corroborates previous findings that stomatal conductance is very sensitive to saline water irrigation (Orsini et al., 2013; Marsic et al., 2018; Massai et al., 2004). The stomatal conductance of tomato and grafted plants responded to saline water irrigation through stomatal closure, but the decrease in the grafted plants did not reach the same degree as in tomato plants. This may be due to the grafted plants' response to saline water irrigation, and these mechanisms are well supported in salt-resistant coastal species (Naumann et al., 2007). This confirms the grafted plants' stomatal regulation efficiency. These results were consistent with Penella et al. (2016), who also showed photosystem tolerance of grafted plants with reduced non-stomatal limitation. Moreover, the photosynthetic apparatus was not stressed in the grafted or tomato plants, due to the absence of alterations in ETR and NPQ (Table 2) under either irrigation. These observations agree with the findings of He et al. (2009) and Pal et al. (2016) in tomato. In addition, gas conductance in the leaf (stomatal conductance) increased due to altered root morphology, i.e., increased radial conductivity of the thinner rooted rootstock, allowing for increased root hydraulic conductivity (Suchoff et al., 2017).

The root diameter and root mass density of the grafted plants were not reduced by saline water irrigation, suggesting that the lack of change in root thickness with a consequent increase in root length density is a tolerance response to saline water irrigation (Lovelli et al., 2012). In addition, thin, dense roots allow osmotic adjustment to salinity stress without having to change the photosynthate partitioning in the root tips (Snapp and Shennan, 1992). In the grafted plants, the root volume was reduced under saline water irrigation, but this reduction was negligible compared to potato. Current reports propose that shoot-derived compounds can alter root morphology (Suchoff et al., 2017; Spiegelman et al., 2015).

The root diameter and volume of the grafted plants were not affected in the surface (0–15 cm) or subsurface (15–45 cm) soils (Fig. 3), aiding in mineral (K, Ca, Mg) uptake (Table 2) under saline water irrigation. This is in contrast to Min et al. (2014) who reported that N application with salinity reduces the root volume and diameter at 0–20 cm soil depth. Moreover, the increase in root length density and unaffected root mass density of the grafted plants may be an adaptation to saline water irrigation in the subsurface soil (15–30 cm soil depth) (Fig. 2). The reported root response further confirms Salehi-Mohammadi et al.'s (2009) finding that the fine roots in the subsurface influence the uptake of minerals, enhancing mineral uptake.

Plant growth under salinity is inhibited initially by osmotic stress and later by mineral stress (Munns and Tester, 2008), both of which may be modified by the rootstock and scion characteristics (Martínez-Ballesta et al., 2010). Accumulation of Na in the stems of the tomato and grafted plants was similar due to the higher transpiration, which enhanced Na uptake under saline irrigation; this corroborates the findings of Munns and Tester (2008). Rootstocks affect the Na concentration of the scion by directly impacting its uptake and transport (Amiri et al., 2014) through ion exclusion or retention. Indeed, in this study, the Na load in the grafted plant leaves was reduced, whereas the K load and the K/Na ratio were better preserved under saline water irrigation (Table 2). Potato rootstock can regulate the transport of Na to the shoot by sodium exclusion and retention, which corroborates previous reports of Albacete et al. (2009); Colla et al. (2010) and Edelstein et al. (2016), who found that Na exclusion by the rootstock enhances scion tolerance.

Increased activities of plasma membrane H^+-ATPases (PMA) and Na^+/H^+ antiporter (SOS1) may have enabled cucumber rootstock to pump Na into the vacuole, preventing its accumulation in pumpkin scion (Lei et al., 2014). This was followed by non-significant tuber Na accumulation in grafted plants under saline water irrigation which safeguarded the scion from the adverse effects of Na. These mechanisms were further strengthened by the present findings with increased uptake of K, Ca and Mg ions in the scion, leading to small osmotic potentials with low energy cost. The K and Mg concentrations decreased in the leaf and stem of tomato vs. potato plants under saline water irrigation. These results followed previous reports of Giuffrida et al. (2009) and Grattan and Grieve (1999). However, these negative consequences were not evident in the grafted plants with superior fruit K, Ca and Mg concentrations under saline water irrigation, further supporting the findings of Grattan and Grieve (1999) and Savvas et al. (2011). The grafted plants showed lower reductions in fruit Ca, possibly due to the clear interaction between the potato rootstock and tomato scion, in agreement with recent observations made by Giuffrida et al. (2014). Increased leaf K and Mg, and unchanged leaf Ca concentrations have been related to better osmotic adjustment under saline water irrigation (Penella et al., 2016), which was confirmed by the change in leaf osmolality (Table 2) in the present study.

The K/Na ratio in plant compartments is an indicator of the plant's ability to use K ions under salinity (Santa-Cruz et al., 2002), to the extent that the maintenance of a high K/Na ratio is important for salinity tolerance. The leaf and fruit K/Na ratios of the grafted plants was higher (twofold and threefold, respectively) than those of the tomato plant, in line with Munns and Rawson (1999) who confirmed that a ratio greater than 1 is considered better for metabolic activity. Higher Mg/Na and Ca/Na ratios were observed in the fruit and leaves of grafted plants under saline water irrigation (Table 2), in agreement with Di Gioia et al. (2013); Santa-Cruz et al. (2002), and Savvas et al. (2011), who provided evidence of grafted plants' ability to limit ionic imbalances under saline water irrigation.

The grafted plants showed a higher capacity to modulate Na, Ca, Mg and K partitioning by reducing Na accumulation and increasing that of the other cations in leaves and fruit, thus enabling the maintenance of higher K/Na, Ca/Na and Mg/Na ratios. This positive effect of potato rootstock on the tomato scion with respect to salinity tolerance may be due to its better compatibility for grafting. These findings are in accordance with Martínez-Rodríguez et al. (2008), who confirmed that shoot salt tolerance depends on the root system.

The graft combinations with potato rootstock and tomato scion tended to present unaffected fruit yield compared to tomato under non-saline water irrigation, which corroborates previous yield responses obtained with different grafted tomato genotypes (Estan et al., 2005; Martínez-Rodríguez et al., 2008). Passam et al. (2005) reported that the similar fruit yield of tomato on eggplant rootstock was due to higher fruit mass. Trajkova et al. (2006) reported that fruit yield was affected by increasing salinity, whereas yield reduction might have been due to fruit mass. In contrast, the potato rootstock allowed the scion to produce not different fruit yield and fruit mass (compared to the tomato) under saline water irrigation (Fig. 4). Recent reports from Fullana-Pericàs et al.

(2018) and Zeist et al. (2017) also found no variation in yield responses in tomato grafted on wild solanum (*Solanum pimpinellifolium*) rootstock under drought conditions. Fruit TSS content was similar in the grafted and tomato plants under saline water irrigation, corroborating previous findings by Di Gioia et al. (2010) and Savvas et al. (2011), who reported that increased fruit TSS represents better fruit quality under saline water irrigation. Saline water irrigation reduced the size and yield of the tubers in the potato and grafted plants. However, there was no significant reduction in size, number or yield of the grafted plants in comparison to potato plants. This is in agreement with Levy (1992) who reported no variation in tuber yield, and tolerance to intermediate to severe salinity.

The present findings are supported by a recent report (Xia et al., 2018) on long-distance movement of genetic materials (mRNA) that have physiological roles in the tomato–potato graft system. It principally occurs through the process of photosynthesis, which uses light as its source of energy (Trifonov et al., 2018). Overall, the water productivity of the grafted plant was superior to that of control (by 70.5 % and 56.8 %) under non-saline and saline water irrigation, respectively (Table 3). Thus, use of potato rootstocks could be a promising approach to reducing the negative effects of saline water irrigation, in agreement with Penella et al. (2013) findings on pepper under salinity stress.

5. Conclusions

The present study provides a detailed understanding of how tomato scion grafted on potato rootstock enhances tolerance and yield performance under saline water irrigation. The grafted plants provided fruit aboveground and tubers belowground with a total dry mass that was unaffected by irrigation type. Saline water irrigation affected both the fruit yield of tomato and grafted plants, and tuber yield. Under the same irrigation water quality, the grafted plants produced similar fruit yield of tomato and tuber yield of potato in the same plant. In addition, the grafted plants showed modified dry mass allocation, unaltered leaf physiology, and improved Na, Ca, Mg and K partitioning from root to fruit, while the root morphological traits were unaffected. The grafted plants improved water productivity and possibly may increase fertilizer use efficiency. These results suggest that the use of potato rootstock may be a good strategy for increasing tolerance to saline water irrigation, as well as the production of both fruits and tubers in a single plant. Above all, even though the grafted plants were grown in sandy loam with similar fertilizer application, grafting still increased tomato's tolerance under saline water irrigation. Potato may be considered as a potential and profitable rootstock for grafted tomato cultivation in poor-quality-irrigated arid environments. Moreover, scaling up to other solanaceous vegetables should be the goal of future research with potato rootstock. The present experiment could be applied to processing-tomato cultivation under field conditions, where the combined harvesting of tomato and potato is possible.

Author contributions

T.P., J.E., and N.L commonly conceptualized the manuscript. Evaluation of data and writing of the original draft were done by T.P. Reviewing and correction of the manuscript was done by J.E. and N.L.

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.

Funding

This research was supported by the Israel Ministry of Agriculture and Rural Development(Eugene Kandel Knowledge Centers) as part of the "Root of the Matter: The root zone knowledge center for leveraging modern agriculture".

Acknowledgments

The authors acknowledge the valuable contributions of Liron Summerfield for help with the grafting and measurements, Yuval Shani for his skillful assistance with the greenhouse work and Dr. Amos Russak for help with the mineral analysis. We are also grateful to Ori Mishli, Kibbutz Yotvata Field crops for providing the potato tubers.

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.2021.110050.

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