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Growth and Gas Exchange in Grafted Tomato: Impact of Rootstock Type and Irrigation Practices

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ABSTRACT

This study evaluated the effects of irrigation regimes (well-watered, wet–dry, and dry-down conditions) and grafting (using high- and low-vigor rootstock genotypes: Maxifort, Unifort, and Beaufort, grafted onto the commercial cultivar ‘Money Maker’) on tomato growth, gas exchange (stomatal conductance and photosynthesis), and water-use efficiency (WUE). Results showed that irrigation regime, particularly the dry-down treatment, enhanced root and shoot biomass, leaf total soluble sugar content, stomatal conductance, and photosynthetic CO_2 assimilation compared to the well-watered treatment. Grafted plants exhibited greater root and shoot biomass, stomatal conductance, photosynthetic CO_2 assimilation, and both instantaneous (A/E) and intrinsic (A/gs) WUE, with responses varying by rootstock genotype and soil moisture status. Under well-watered conditions, instantaneous WUE was highest in non-grafted scions and lowest in Unifort, whereas under wet–dry conditions it was highest in Maxifort and lowest in Unifort. Overall, grafting modified growth and physiological traits and appeared to enhance tolerance to root-zone water-deficit stress. These growth and physiological attributes provide valuable criteria for selecting rootstock–scion combinations to improve performance under variable irrigation levels. Accordingly, irrigation management and grafting strategies can be adopted to enhance drought tolerance and water-use efficiency (i.e., water-saving capacity) in tomato.

Introduction

Tomato (*Lycopersicum esculentum* L. Mill.) is an edible berry belonging to the family Solanaceae. Globally, tomato production has reached nearly 186.82 million tons, cultivated on a total area of about 5 million hectares, with an average productivity of 36.97 t ha^{-1} (FAOSTAT, 2018). Tomato fruits are juicy and rich in antioxidants, constituents of great importance to human nutrition and health. In particular, lycopene and other antioxidants have been reported to protect humans against cardiovascular diseases and certain types of cancer (Bin-Jumah et al., 2022). Grafting may involve the use of scion and rootstock from distinct or identical genotypes, or even from different species, resulting in intra-specific and inter-specific grafts, respectively (Rouphael et al., 2016; Gautier et al., 2019; Deepak et al., 2019). It is a common practice in both woody plants (trees and shrubs) and herbaceous annual plants, especially members of the Solanaceae family. Over the last few decades, commercial vegetable production has experienced renewed research interest and expanded application of grafting technology (Rouphael et al., 2016; Belmonte-Ureña et al., 2020). Rootstock genotypes are recognized for their capacity to influence scion performance in terms of growth, yield, water use (uptake and efficiency), and resistance to diseases (Van Leeuwen and Seuin, 2006; Albacete et al., 2015). Furthermore, rootstocks play an important role in regulating the performance of grafted plants

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under variable climatic conditions, while also influencing product quality and marketability (Albacete et al., 2015; Zhang et al., 2019; Opazo et al., 2019; Hernandez-Espinoza et al., 2020). As such, grafting has been reported to provide opportunities for adapting plants to a wide range of stressful environments, including drought, soil salinity, heavy metal toxicity, extreme temperatures, and biotic stress conditions (Agele and Cohen, 2008; Rouphael et al., 2016; Mir et al., 2023).

These beneficial attributes of grafting are largely associated with grafting-induced modifications in root–shoot relationships and physiological functions in plants (Bauerle et al., 2008; Bristow et al., 2021; Mir et al., 2023). According to Loviso et al. (2010) and Belmonte-Ureña et al. (2020), the characteristics of rootstock and scion genotypes can modify phenotypic traits and physiological processes that are crucial for stress tolerance in plants. Rootstocks regulate plant water use through modifications in water and nutrient uptake capacities, with consequences for root development, water transport (xylem hydraulics) (Agele and Cohen, 2008; Alsina et al., 2011; Bristow et al., 2021), gas exchange (Jones, 2012; Marguenta et al., 2012; Usanmalla et al., 2019), and above-ground development (Fullana-Pericas et al., 2019; Vougeleka et al., 2023; Barbagallo et al., 2008; Schwarz et al., 2010). Rootstock and scion genotypes can therefore be selected to enhance the performance of grafted plants in specific climatic conditions or to achieve targeted marketing objectives (Opazo et al., 2019; Bauerle et al., 2021). Improved understanding of the functional physiology of grafted plants under abiotic stress conditions, particularly moisture deficits, is essential for informed decision-making in the choice of rootstock–scion combinations for specific environments (Belmonte-Ureña et al., 2020; Van Leeuwen and Seguin, 2006).

In the era of climate change, manifested in increased water scarcity and soil moisture deficits, grafting has become increasingly relevant for improving plant tolerance to drought stress (Barbagallo et al., 2008; Schwarz et al., 2010). Climate change and extreme weather events—such as drought (soil moisture deficits) and temperature rise—have intensified competition for water resources among agriculture, industry, and urban sectors. This challenge underscores the urgent need for improved water management practices, especially in agriculture and vegetable cultivation. Drought and soil moisture deficits disrupt multiple levels of plant metabolism (Bristow et al., 2021; Loviso et al., 2010; Schwarz et al., 2010). One potential strategy to mitigate these challenges lies in grafting, specifically through the use of rootstock and scion genotypes capable of alleviating soil and atmospheric moisture stress in plants (Albacete et al., 2015; Schwarz et al., 2010; Ahmed et al., 2021). Thus, improved insights into the mechanisms underlying rootstock effects on growth, physiology, and water productivity of tomato under variable soil moisture conditions are crucial. Limited soil moisture can also affect nutritional quality parameters of tomato fruit, including total soluble solids, soluble sugars, organic acids, and vitamin C. In addition, other important fruit quality traits such as dry matter content, dietary fiber, and carbohydrates are influenced by water availability (Bristow et al., 2021; Schwarz et al., 2010; Warschefsky et al., 2016). There is increasing interest in the use of rootstock genotypes for grafting to improve drought tolerance in vegetable production, owing to the potential of grafted plants to enhance water-use efficiency while maintaining key scion quality traits (Opazo et al., 2019; Schwarz et al., 2010; Ahmed et al., 2021). However, large variability in rootstock responses to water deficits has been reported in vegetables, highlighting the need to better understand the physiological and genetic mechanisms underlying drought tolerance (Schwarz et al., 2010; Zhang et al., 2016). This study was conducted to examine the physiological responses of grafted tomatoes to different irrigation levels, thereby establishing variable root-zone moisture statuses. Also, the aim was to identify key physiological root- and scion-derived traits in tomatoes grafted onto various rootstock genotypes under variable root-zone water statuses.

Materials and Methods

A study was designed to investigate the effects of rootstock genotype and root-zone moisture deficit on growth and gas exchange variables of tomato. The experiment was conducted in the laboratories and greenhouse of the Leibniz Institute of Vegetable and Ornamental Crops (IGZ), Großbeeren, Germany (decimal latitude and longitude: 52.35862, 13.30994).

Growth conditions and treatments

Seeds of tomato genotypes (scion and rootstock) germinated in polystyrene trays filled with a peat-based substrate in a greenhouse chamber measuring 100 m in width, 22 m in length, and 4 m in height. Seedlings of the commercial tomato cultivar *Money Maker* were grafted onto three rootstocks with contrasting vigor: Maxifort (high vigor), Unifort (low vigor), and Beaufort (moderate vigor). In addition, non-grafted and self-grafted ‘Money Maker’ plants were included as controls (Schwarz, Dietmar: Personal communication).

Tomato seedlings were subjected to three irrigation regimes: (i) well-watered (continuous hydration), (ii) wet–dry (repeated wetting and drying cycles), and (iii) dry-down (a single prolonged drought phase). In the well-watered treatment, plants were maintained at field capacity through sustained irrigation. The wet–dry treatment involved once-weekly irrigation to replenish soil moisture losses, thereby imposing alternating wetting and drying cycles. In the dry-down treatment, water was withheld for an extended period, with re-irrigation applied fortnightly to allow partial recovery from severe root-zone moisture deficits. Irrigation treatments were imposed two weeks after plant establishment in the greenhouse. For each irrigation regime, independent cohorts of plants were used for soil and plant measurements, which began two weeks after initiation of the treatments. These irrigation strategies successfully induced differences in soil (root-zone) moisture status. Grafting was performed 30 days after seed germination, at which time tomato plants had developed their third true leaf, using the tube-grafting method. Immediately after grafting, plants were placed in a closed plastic tunnel within the greenhouse to maintain relative humidity close to 100% and a microclimate temperature of 20–22 °C. Seven days before transplanting into pots, the plastic tunnel was removed, and grafted plants were acclimated under ambient greenhouse conditions. To ensure uniform plant size at transplanting, seeds of the non-grafted treatment were sown two weeks later than the grafted treatments. Following transplanting, tomato plants were irrigated with nutrient solution and fertigated daily using a computerized, automated drip fertigation system.

Soil moisture measurement

Volumetric soil water content was measured between 13:00–15:00 using a time domain reflectometer (TDR 100, Campbell scientific). The TDR probes (35 cm in length) were installed for separate measurements of the root-zone moisture of the tomato plants that were irrigated with different irrigation regimens. Soil moisture content for the different tomato plant types subjected to the three irrigation regimes (well-watered, wet–dry cycle, and dry-down) was recorded during the measurement period from 13 to 27 November (Fig. 1a–c).

Measurement of gas exchange variables

After subjecting tomato plant types (self-grafted, grafted using variable rootstock–scion combinations, and non-grafted) to different root-zone moisture regimes, gas exchange variables—including photosynthetic CO_2 assimilation (A), intercellular CO_2 concentration (Ci), stomatal conductance (gs), transpiration (E), instantaneous water-use efficiency (A/E), and intrinsic water-use efficiency (A/gs)—were measured. Physiological variables related to gas exchange and water-use efficiency were assessed using five leaflets from the middle canopy of each plant (third or fourth leaf from the apex), as these leaves are expected to exhibit maximum photosynthetic capacity (Wang et al., 2019). Measurements were taken during mid-morning to early afternoon (1100–1300 h) under greenhouse conditions using a portable infrared gas analyzer (IRGA; model LI-6800, LiCOR, Lincoln, NE, USA). Net photosynthesis rate (A, μmol m^{-2} s^{-1}), transpiration (E, mmol m^{-2} s^{-1}), leaf temperature (°C), and stomatal conductance (gs, mol m^{-2} s^{-1}) were measured at a photosynthetically active radiation (PAR) of 1500 μmol m^{-2} s^{-1}. Leaf and cuvette temperatures were maintained at 25 °C, vapor pressure deficit was stabilized at ~1.2 kPa, and the reference CO_2 concentration was set at 390 μmol mol^{-1}. Additional measurements included intercellular CO_2 concentration (Ci), and the efficiency of carboxylation was calculated as the ratio of A to Ci (Zhang et al., 2016). Water-use efficiency (WUE) parameters were derived from the gas exchange data following Hatfield and Dold (2019). Instantaneous WUE was calculated as the ratio of A to E (A/E), while intrinsic WUE was calculated as the ratio of A to gs (A/gs).

Starch content: extraction and analysis

The total leaf sugar contents (glucose, fructose, and sucrose) were measured following the methods described by Araza et al. (2006) and Chow and Landhouser (2004). Leaf starch content was determined through starch extraction and analysis using the Total Starch Assay Kit (Sigma-Aldrich). Simultaneous separation and quantification of fructose, glucose, and sucrose in tomato leaves were performed using high-performance liquid chromatography (HPLC; DW-LC1620A) coupled with evaporative light scattering detection (ELSD; ELSD-LT III). The HPLC-ELSD conditions were optimized according to Araya et al. (2006). Peak identification and quantification were conducted using calibration standards of HPLC-grade sugars, namely glucose, fructose, and sucrose (Sigma-Aldrich). The mineral contents of tomato leaves were analyzed following the procedures of IITA (1978) and AOAC (2012). Leaf samples from the treatments were collected, oven-dried at 80 °C for 48 h, and ground. The mineral constituents were determined after digesting the samples at 300 °C in a mixture of hydrogen peroxide, sulfuric acid, selenium, and salicylic acid (IITA, 1978). The digests were analyzed for total N, P, K, Na, Ca, and Mg. Total N was determined as total Kjeldahl nitrogen (AOAC, 2012). Total phosphorus was quantified using the ascorbic acid–blue color method, with absorbance measured at 880 nm using a UV spectrophotometer. Calcium, potassium, and magnesium contents in a 1/20 dilution (sample/distilled water) of the plant digests were measured using an Atomic Absorption Spectrophotometer at wavelengths of 766.5, 422.7, and 285.2 nm, respectively. Sodium content in the diluted samples was determined at an absorbance of 248.3 nm (IITA, 1978).

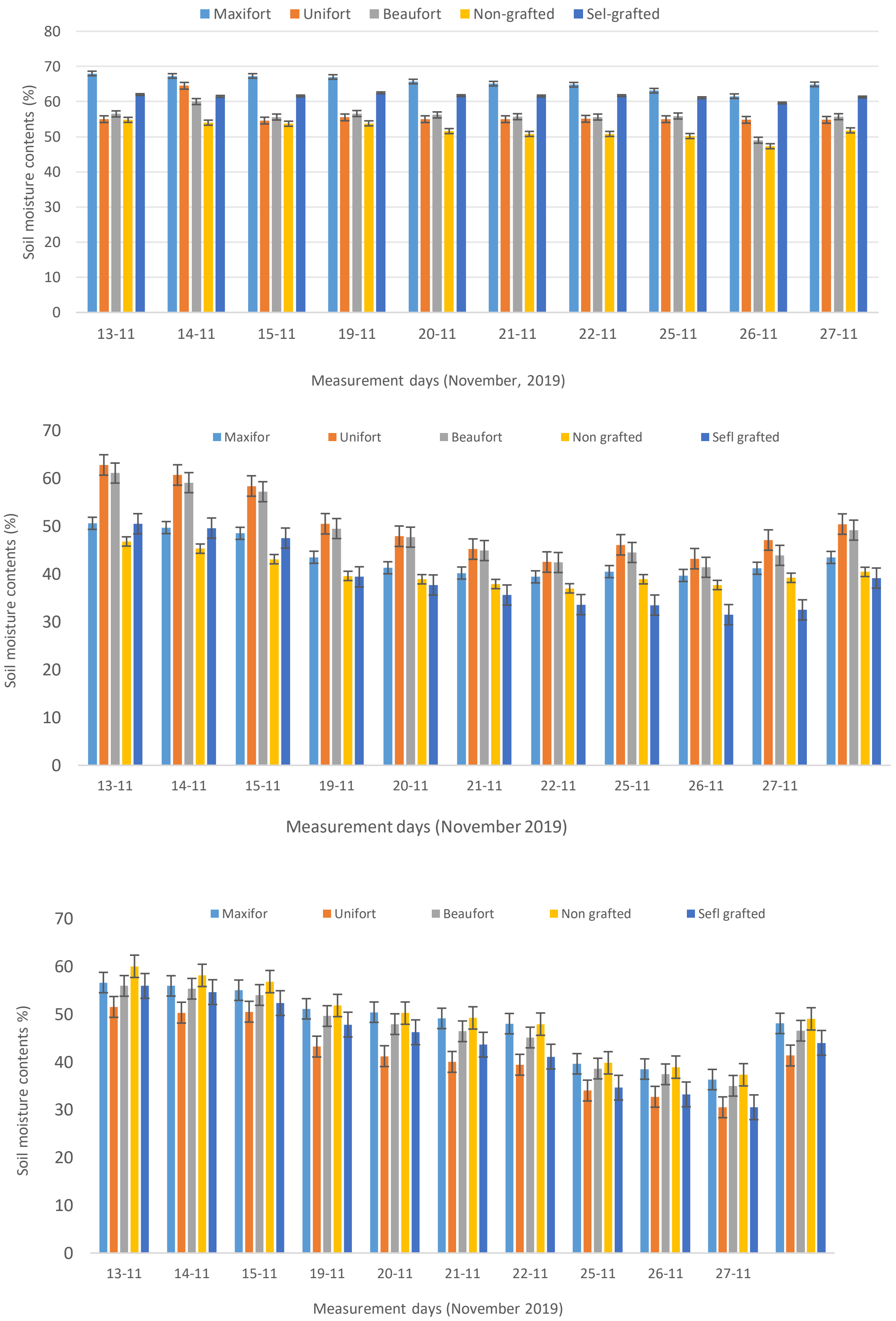

Fig. 1. Soil moisture content of tomato plants measured with TDR probes from 13 to 27 November under different irrigation regimes: (a) well-watered, (b) wet–dry cycle, and (c) dry-down.

Root and shoot biomass yield

Tomato plants were sampled at the flowering stage for root and shoot biomass measurement. Fresh weights of roots and shoots were recorded, and the root-to-shoot ratio was calculated. Roots were rinsed with tap water, blotted dry, and weighed. Dry weights of roots and shoots were determined after oven-drying at 70 °C to a constant mass.

Experimental design and analysis

The experiment followed a 3 × 5 factorial arrangement of irrigation regime and plant type (grafted and non-grafted), established using a completely randomized design. The irrigation regime–plant type combinations were randomly distributed within the greenhouse. Data were analyzed using two-way analysis of variance (ANOVA). For post-hoc comparisons, Fisher's Least Significant Difference (LSD) test was applied to assess differences among treatment means at the 5% probability level. Statistical analyses were conducted under the assumptions of normality and homogeneity of variance; therefore, data were tested for both. Where required, all measurements were performed in triplicate to ensure accuracy and reproducibility. In the tables, treatment groups that were not significantly different share the same letters within columns.

Results

Irrigation regime and tomato plant type on soil moisture contents

In Figure 1a–c, the effects of irrigation regimes on soil moisture content across tomato plant types are presented. Under the dry-down treatment, the lowest soil moisture content was observed for Unifort, while Maxifort and Beaufort exhibited higher and comparable values. Under the wet–dry condition, soil moisture content was highest for Unifort, followed by Beaufort, and lowest for Maxifort. By contrast, under the well-watered condition, Maxifort exhibited the highest soil moisture content, while Beaufort had the lowest.

Across tomato plant types (grafted, self-grafted, and non-grafted), soil moisture content under dry-down conditions was highest in non-grafted plants and in Maxifort, whereas the lowest value was recorded for Unifort. Under the wet–dry condition, soil moisture was again highest in Unifort and lowest in Maxifort, with no significant differences between self-grafted and non-grafted plants. Among rootstock genotypes under well-watered conditions, Maxifort exhibited the highest soil moisture, while Beaufort and Unifort showed statistically similar values (Fig. 2). Consistently, Maxifort maintained higher root-zone moisture under well-watered conditions, whereas Beaufort had the lowest.

In contrast, under the wet–dry regime, Unifort maintained the highest root-zone moisture at most measurement dates. Under the dry-down treatment, Unifort exhibited lower soil moisture compared to Maxifort and Beaufort, though the latter two did not differ significantly (Fig. 2).

Overall, under well-watered conditions, soil moisture content decreased in the order Maxifort > Unifort > Beaufort. Under the wet–dry regime, values decreased in the order Unifort > Beaufort > Maxifort, while under the dry-down treatment, the order was Maxifort > Beaufort > Unifort. On average, soil moisture content across treatments was 66.4%, 52.6%, and 44.4% under well-watered, wet–dry, and dry-down conditions, respectively.

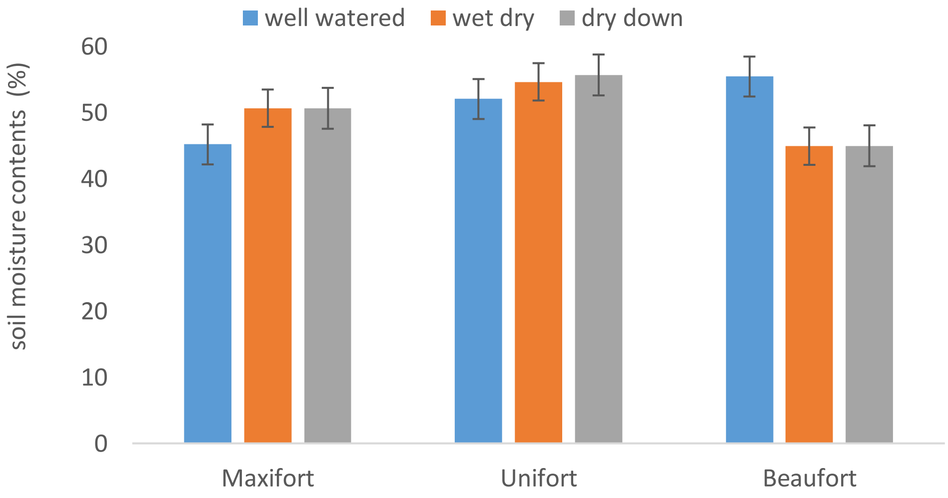

Fig. 2. Effect of irrigation levels on soil moisture contents of tomato rootstock genotype.

Irrigation regime and tomato plant type on leaf concentrations of mineral and sugars, as well as root and shoot biomass

The effects of irrigation regime and tomato plant type on biomass yields and leaf sugar contents is presented in Table 1.

Biomass yields

Root biomass was highest under the wet–dry irrigation regime, whereas shoot biomass was greatest under well-irrigated conditions, followed by wet–dry, and lowest under the dry-down treatment. Significant differences in root and shoot biomass accumulation were observed among tomato plant types. Non-grafted plants produced the heaviest root biomass, followed by plants grafted onto Maxifort rootstock, while the lowest root biomass was recorded for Beaufort (Table 1).

Table 1. Effects of irrigation regime and tomato plant type on biomass weight and leaf sugar contents.

Treatments	Root fresh weight (g)	Root dry weight (g)	Shoot fresh weight (g)	Shoot dry weight (g)	Glucose (mg/leaf dry weight)	Fructose (mg/leaf dry weight)	Sucrose (mg/leaf dry weight)	Sugars (mg/ leaf dry Weight)
Irrigation								
Well-irrigated	6.48	5.78	290.28	16.77	2.582	2.062	2.127	6.771
Wet-dry	6.84	6.06	303.64	18.45	1.932	1.567	2.098	5.597
Dry down	5.64	5.23	245.25	15.33	5.935	4.827	3.993	14.768
LSD (0.05)	0.051	0.022	0.019	0.019	0.0017	0.0061	0.0012	0.0073
Plant type								
Non grafted	6.99	5.92	298.99	17.72	3.346	3.425	2.876	10.648
Self-grafted	6.65	6.13	289.42	17.75	3.548	2.792	2.712	9.053
Beaufort	5.43	5.02	249.26	14.96	2.475	2.124	2.531	7.136
Unifort	5.92	5.06	252.11	15.28	3.195	2.374	2.821	8.291
Maxifort	6.75	5.99	308.85	18.53	3.849	3.477	2.755	10.082
LSD (0.05)	0.027	0.302	0.332	0.332	0.381	0.352	0.461	0.585
Irrigation by plant type interaction	*	ns	*	ns	*	ns	*	ns

*, significant at 5 % probability level; ns, non-significant.

Leaf sugar concentrations

Soil moisture deficits significantly increased leaf sugar concentrations, particularly glucose and fructose, compared to well-irrigated tomatoes (Table 1). Grafted plants accumulated more glucose and sucrose under low soil moisture conditions than under well-irrigated conditions. However, under well-irrigated treatment, the total soluble sugar content was higher than in plants exposed to root-zone moisture deficits. Leaf glucose concentration was highest under the dry-down treatment and lowest under the wet–dry regime, while fructose and sucrose were also greatest under dry-down compared to well-irrigated conditions (Table 1). Overall, total sugar concentrations were significantly higher under dry-down irrigation. Among tomato plant types, glucose content was highest in self-grafted plants and lowest in Beaufort, fructose was greatest in self-grafted and Maxifort plants, while the total soluble sugar concentration was highest in non-grafted and Maxifort plants and lowest in Beaufort. Root and shoot biomass were also influenced by irrigation regimes and tomato plant types.

Leaf mineral concentrations

Leaf mineral concentrations varied with irrigation regime and tomato plant type (Table 2). Nitrogen concentration was highest under wet–dry and dry-down conditions, carbon under dry-down, calcium (Ca) and potassium (K) under well-irrigated conditions, sodium (Na) under well-irrigated conditions, and phosphorus (P) under both well-irrigated and wet–dry conditions.

Among tomato plant types, nitrogen was highest in Unifort, followed by Maxifort and Beaufort, and was also elevated in non-grafted and self-grafted plants, while the lowest concentration was observed in Maxifort. The C: N ratio was greatest in non-grafted and self-grafted plants. Calcium concentration was highest in self-grafted and Maxifort plants. Potassium (K) and magnesium (Mg) were highest in Beaufort, followed by Unifort and Maxifort. Sodium was greatest in self-grafted plants, while phosphorus (P) was highest in Unifort, followed by non-grafted and self-grafted plants.

Table 2. Effects of irrigation regime and tomato plant type on leaf chemical (mineral) contents.

Treatments	**Total N (%)**	**Total carbon (%)**	**C/N ratio**	**N (g kg^{-1})**	**Ca (g)**	**K (g)**	**Mg (g)**	**P (g)**
Irrigation								
well-irrigated	5.244	34.188	6.526	52.43	23.92	85.643	2.61	8.97
Wet-dry	5.301	34.371	6.494	53.01	23.96	85.494	2.76	8.92
Dry down	5.437	34.921	6.429	54.38	22.26	82.109	2.68	8.55
LSD (0.05)	0.02	0.022	0.008	0.092	0.007	0.0018	0.214	0.007
Plant type								
Non grafted	5.242	34.832	6.648	52.420	23.57	81.51	3.175	8.879
Self-grafted	5.267	34.572	6.573	52.670	24.14	81.01	3.182	8.828
Beaufort	5.321	34.468	6.486	53.208	22.08	88.61	2.212	8.807
Unifort	5.486	34.456	6.287	54.862	22.70	85.03	2.392	8.912
Maxifort	5.322	34.139	6.421	53.225	24.43	85/96	2.509	8.647
LSD (0.05)	0.14	0.102	0.093	0.177	0.001	0.005	0.0012	0.454
Irrigation by plant type	*	^{ns}	^{ns}	*	*	*	^{ns}	^{ns}

*, significant at 5 % probability level; ^{ns}, non-significant.

Irrigation regime and grafting on gas exchange variables of tomato gas exchange

The internal CO_2 concentration (Ci) was highest under the dry-down treatment and lowest under well-irrigated conditions, whereas photosynthetic rate (A) and stomatal conductance (gs) were highest under well-irrigated conditions and lowest under the wet–dry regime (Table 3). Instantaneous water use efficiency (A/E) was greater in well-irrigated plants than in those under wet–dry or dry-down treatments. In contrast, intrinsic water use efficiency (A/gs) was highest under the wet–dry regime, followed by well-irrigated, and lowest under dry-down conditions. Among tomato plant types, the photosynthetic rate (A) increased in the order: self-grafted > Unifort > Maxifort > Beaufort > non-grafted. For stomatal conductance (gs), the order was: Maxifort > Beaufort > non-grafted > Unifort. Overall, gs was highest in Maxifort, lower in Unifort, and lowest in non-grafted plants. Internal CO_2 concentration (Ci) was greatest in self-grafted and Unifort plants, and lowest in self-grafted plants. For internal leaf water vapor concentration (PCi), the highest values were recorded in non-grafted plants and the lowest in self-grafted tomatoes. The ratio of A/Ci, which reflects the relative control of A by carboxylation capacity and CO_2 supply, was higher under well-irrigated and wet–dry conditions compared to the dry-down treatment.

Table 3. Effects of irrigation regime and plant type on gas exchange variables of tomato.

		Transpiration (µmol m^{-2} s^{-1})	**Photosynthesis (µmol m^{-2} s^{-1})**	**Ca (µmol m^{-2} s^{-1})**	**Ci (µmol m^{-2} s^{-1})**	**Pci**	**VPD (leaf) (kPa)**	**A/E**	**A/gs**	**A/Ci**
Plant type	Non-grafted	0.0046	9.217	397.072	362.95	36.685	1.396	1974.45	25.956	0.025
	Self-grafted	0.0046	9.255	397.025	362.19	36.607	1.395	1984.13	26.074	0.025
	Beaufort	0.0046	9.209	397.036	362.61	36.651	1.396	1966.84	25.855	0.025
	Unifort	0.0045	9.255	397.072	362.93	36.681	1.395	1989.28	26.147	0.025
	Maxifort	0.0047	9.251	397.038	362.70	36.659	1.395	1966.84	25.834	0.025
	STD Error (SE)	0.00001	0.01026	0.00987	0.1372	0.0139	0.0005	4.53505	0.0610	0.0003
Irrigation regime	Plant types	Transpiration (µmol m^{-2} s^{-1})	Photosynthesis (µmol m^{-2} s^{-1})	Ca (µmol m^{-2} s^{-1})	Ci (µmol m^{-2} s^{-1})	Pci	VPD (leaf) (kPa)	A/E	A/gs	A/Ci
Well-irrigated	Non-grafted	0.0041	9.208	397.045	363.47	36.736	1.396	1928.54	25.317	0.0250
	Self-grafted	0.0051	9.198	397.047	363.69	36.757	1.395	1920.35	25.193	0.0252
	Beaufort	0.0041	9.188	397.043	363.64	36.751	1.394	1913.82	25.088	0.0252
	Unifort	0.0048	9.150	397.053	363.87	36.774	1.394	1903.50	24.941	0.0251
	Maxifort	0.0048	9.099	397.072	364.16	36.802	1.394	1891.35	24.777	0.0250
	STD Error	0.00006	0.02005	0.0062	0.1164	0.0113	0.0004	0.00064	0.0943	0.00062
Wet-Dry	Non-grafted	0.00481	9.034	397.08	364.31	36.816	1.395	1876.49	24.595	0.02479
	Self-grafted	0.00482	9.028	397.08	364.37	36.822	1.396	1871.93	24.547	0.02477
	Beaufort	0.00482	9.022	397.07	364.34	36.818	1.396	1870.13	24.534	0.02476
	Unifort	0.00482	9.042	397.07	364.27	36.811	1.395	1873.96	24.572	0.02482
	Maxifort	0.0049	9.063	397.06	363.89	36.772	1.396	1884.57	24.717	0.02492
	STD Error (SE)	0.00004	0.0067	0.00297	0.0876	0.0091	0.0002	2.5212	0.0327	0.00024
Dry Down	Non-grafted	0.0048	9.037	397.05	363.96	36.778	1.396	1882.73	24.702	0.0248
	Self-grafted	0.0047	9.012	397.06	363.99	36.781	1.397	1880.52	24.686	0.0247
	Beaufort	0.0047	8.985	397.06	363.97	36.778	1.398	1879.15	24.688	0.0246
	Unifort	0.0047	8.959	397.07	364.14	36.795	1.397	1872.96	24.591	0.0246
	Maxifort	0.0048	8.970	397.06	364.38	36.819	1.395	1866.12	24.484	0.0243
	STD Error (SE)	0.000004	0.0144388	0.00312	0.0810	0.0078	0.0004	3.01707	0.0417	0.0004
	Irrigation regime	Transpiration (µmol m^{-2} s^{-1})	Photosynthesis (µmol m^{-2} s^{-1})	Ca (µmol m^{-2} s^{-1})	Ci (µmol m^{-2} s^{-1})	Pci	VPD (leaf) (kPa)	A/E	A/gs	A/Ci
Irrigation regime	Well-watered	0.0048	9.043	397.07	364.19	36.805	1.394	1882.29	24.667	0.02483
	Wet-Dry	0.00478	9.014	397.06	363.94	36.777	1.396	1883.67	24.725	0.02476
	Dry-Down	0.0048	8.970	397.06	364.35	36.814	1.394	1867.41	24.486	0.02461
	STD Error (SE)	0.000612	0.0212372	0.00405	0.1189	0.0114	0.0008	5.18053	0.0718	0.00062
Irrigation by plant type		**	**	*	*	ns	*	ns	ns	ns

[*], significant at 5 % probability level; [ns], non-significant.

Water use efficiency

Water use efficiency indicators (instantaneous and intrinsic) varied among tomato plant types. Under well-irrigated conditions, instantaneous water use efficiency (A/E) was highest in non-grafted plants and lowest in Maxifort. Under the wet–dry regime, A/E, which reflects the balance between carbon gain and water cost, was highest in Maxifort, followed closely by non-grafted plants, and lowest in Unifort. For the dry-down treatment, A/E was highest in non-grafted plants, followed by self-grafted tomatoes, and lowest in Maxifort. For intrinsic water use efficiency (A/gs), differences were also observed among rootstock genotypes. Unifort exhibited the highest A/gs, followed by self-grafted and non-grafted plants, while the lowest values were recorded in Maxifort and Beaufort.

Discussion

Irrigation levels and grafting (rootstock–scion combinations) influenced the growth and physiological attributes of tomato. In particular, grafted plants with different rootstock–scion combinations exhibited distinct physiological responses to irrigation regimes, namely adequate irrigation, wet–dry cycles, and dry-down treatments. Leaf sugar contents varied significantly under different irrigation regimes. Under well-irrigated conditions, total sugar concentrations were higher compared with plants exposed to root-zone moisture deficits (wet–dry and dry-down). Previous studies have shown that low soil moisture negatively affects the nutritional quality of vegetables, especially total soluble sugars and solids, organic acids, and vitamin C (Schwarz et al., 2010; Bristow et al., 2021). In the present study, grafted tomato plants accumulated more glucose and sucrose under low soil moisture conditions than under adequate irrigation. Soluble sugar accumulation is known to play a central role in plant defense against water restriction, where sugars act as osmolytes, precursors of energy-related metabolites, and reactive oxygen species (ROS) scavengers, in addition to functioning as regulatory and signaling molecules (Gonzalez-Chavira et al., 2018; Ayre, 2011; Du et al., 2020).

It has been reported that sugars accumulate in the leaves of plants under water deficit as a result of the hydrolysis of stored starch (Ayre, 2011; Du et al., 2022). The elevated glucose content in tomato leaves under root-zone moisture deficits may be attributed to an increased glucose-to-fructose ratio, indicating starch degradation and subsequent reallocation to sugars (Chandra et al., 2012; Chen et al., 2021). High glucose concentrations may also serve as building blocks for osmoprotectants under water-limited conditions (Chandra et al., 2012; Chen et al., 2021).

Evidence from the literature suggests that a key adaptive strategy under soil moisture deficit is the stimulation of starch and sucrose breakdown, followed by carbon allocation in the form of hexoses and pentoses, which provide the building blocks for the biosynthesis of stress-protective compounds (Ayre, 2011; Chandra et al., 2012; Chen et al., 2021). Enhanced accumulation of soluble sugars such as sucrose, glucose, and fructose in leaves may also result from reduced transport of photosynthates to sink tissues (Chandra et al., 2012; Chen et al., 2021). Furthermore, irreversible hydrolysis of sucrose into glucose and fructose under drought stress has been associated with increased expression and activity of acid invertase enzymes in leaves (Du et al., 2020; Chandra et al., 2012; Chen et al., 2021).

Intermittent irrigation treatments—specifically wet-dry and dry-down irrigation with reduced water inputs into the soil—resulted in lower soil moisture contents in the tomato root-zone. On average, these treatments produced 45% and 37% lower moisture contents, respectively, compared to the well-irrigated condition. Such low soil moisture levels can be linked to the reduced growth and physiological performance of tomato under wet-dry and dry-down irrigation. However, these treatments also enhanced the water use efficiency of tomato.

Soil moisture contents varied among tomato rootstock genotypes, an observation attributable to differences in their capacity to extract (deplete) water from the soil under the same irrigation regime. Previous studies have shown that water uptake depends on the rootstock genotype's ability to absorb water, particularly under drought stress (Frioni et al., 2020). Drought stress is known to alter plant morphology, physiology, and biochemistry. Reduced soil moisture availability negatively affects hydraulic functioning (xylem transport), transpiration, photosynthesis, and the uptake and transport of water and nutrients to the shoot system. These modifications in physiological functions ultimately limit plant growth and productivity (Agele et al., 2008; Schwarz et al., 2010).

Tomato growth, measured as biomass yield, declined under both wet-dry and dry-down irrigation treatments compared to well irrigation. The reduced water inputs and the resulting lower soil moisture in the root-zone likely explain the reduced vigor observed in both grafted and non-grafted plants. Poor growth performance under limited soil moisture is also linked to reduced photosynthetic capacity (Schwarz et al., 2010; Pazzagli et al., 2016). This study confirmed that tomato stomatal gas exchange (transpiration and photosynthesis) responds directly to irrigation regimes.

The different irrigation regimes (well irrigation, wet-dry, and dry-down) not only altered soil moisture content but also affected tomato growth and stomatal gas exchange variables. Adequate irrigation maintains favorable soil moisture in the root-zone and ensures internal water balance in plant tissues, with positive effects on transpiration, photosynthesis, and assimilate production. Such a balance fosters optimal growth, water uptake and use, photosynthesis, and metabolite assimilation (Kopoor et al., 2020; Shehata et al., 2022).

Irrigation regimes significantly influenced gas exchange variables, including stomatal conductance (gs), photosynthesis (A), intercellular CO_2 concentration (Ci), carboxylation efficiency (A/Ci), and water use efficiencies (instantaneous (A/E) and intrinsic (A/gs)). Notably, under low irrigation (wet-dry and dry-down) conditions, the tomato rootstock genotypes Maxifort and Unifort demonstrated greater water use efficiency. Such genotypic traits suggest higher tolerance to root-zone moisture deficits. Therefore, Maxifort and Unifort rootstocks appear to be promising materials for tomato breeding aimed at improving tolerance to soil water deficit or drought.

Stomatal closure is widely recognized as the first response of plants under drought conditions. By restricting stomatal opening, plants under water stress maintain favorable water potential and turgor pressure, both of which are critical for survival (Lawlor & Tezara, 2009; Shehata et al., 2022). Previous studies have emphasized that the ability of plants to effectively regulate stomatal aperture is fundamental to survival under fluctuating soil moisture conditions (Milhajevic et al., 2021; Olayemi et al., 2022).

However, stomatal closure inevitably reduces photosynthesis by limiting CO_2 diffusion. Since photosynthesis underpins assimilate production and dry matter accumulation, soil moisture deficit–induced stomatal closure and reduced transpiration have direct consequences for water use efficiency. Shehata et al. (2022) and Pazzagli et al. (2016) reported that increased water use efficiency (a water-saving strategy) is a key outcome of reduced stomatal conductance and photosynthetic activity. Beyond stomatal regulation, plants also deploy physiological and biochemical adjustments as survival strategies under moisture deficit stress (Milhajevic et al., 2021; Olayemi et al., 2022). Reported biochemical responses include stimulation of antioxidant defense systems and the synthesis and accumulation of osmolytes, such as aquaporins (Hemandez-Espinox & Barrious-Masia, 2020; Parkash et al., 2022; Khapte et al., 2022).

In this study, tomato plants grown under root-zone moisture deficits (wet-dry and dry-down treatments) exhibited lower stomatal conductance (gs), internal CO_2 concentration (Ci), and photosynthesis (CO_2 assimilation) compared to well-irrigated plants. A reduction in internal CO_2 concentration can constrain the supply of CO_2 for ribulose-1,5-bisphosphate carboxylase-oxygenase (Rubisco), thereby lowering the activity of enzymes involved in carbon fixation (Dabrowski et al., 2019; Al-Harbi et al., 2018) and ultimately decreasing photosynthetic efficiency (Schwarz et al., 2010; Dabrowski et al., 2019).

The results of the present study are consistent with those of Schwarz et al. (2010) and Pazzagli et al. (2016), who reported decreases in tomato photosynthesis rates from 8.61 to 4.18 $\mu mol\ m^{-2}\ s^{-1}$ under soil moisture deficit. Al-Harbi et al. (2018) and Liu et al. (2023) attributed the reduced stomatal conductance and CO_2 assimilation observed in drought-stressed plants to impaired physiological and biochemical processes in CO_2 fixation. Similarly, Ahmed et al. (2021) and Liu et al. (2023) demonstrated that root-zone moisture deficits adversely affect stomatal conductance, photosynthesis, and related biochemical functions by reducing the maximum quantum yield of PSII photochemistry, the electron transport rate, and the effective quantum yield of PSII photochemistry.

Tomato rootstocks exhibited differences in gas exchange variables and water use efficiencies under the imposed irrigation regimes. These differences may be linked to the capacity of rootstocks to regulate growth and gas exchange in response to irrigation-induced variation in soil water status (adequacy or deficit). The genetic potential of rootstocks is known to influence transpiration in grafted plants under water deficit conditions (Albacete et al., 2015; Warschefsky et al., 2016), a response largely attributed to differences in root hydraulic conductance for water and nutrient transport to the shoot system (Weng et al., 2000; Marguerit et al., 2012; Opazo et al., 2020).

In crops, rootstock genotype plays a crucial role in shaping scion performance, including growth, water relations, water use efficiency, and drought tolerance (Lopez-Marin et al., 2017; Casmali et al., 2021). Grafting has been shown to modulate plant responses to environmental stresses, including soil moisture deficit in the root-zone (Rouphael et al., 2016; Schwarz et al., 2010). In the present study, grafted tomato plants demonstrated enhanced water use efficiencies despite exhibiting reduced photosynthesis, stomatal conductance, and transpiration under soil moisture deficit conditions (wet-dry and dry-down treatments).

Both intrinsic and instantaneous water use efficiencies improved under moisture deficit across all tomato plant types (grafted and non-grafted). However, photosynthesis and internal CO_2 concentration varied among the plant types (grafted, self-grafted, and ungrafted). Previous studies have similarly reported that combinations of tomato rootstock and scion genotypes regulate growth and gas exchange responses (Rouphael et al., 2016; Fullana-Pericas et al., 2020; Ahmed et al., 2021). Rootstock genotype also exerts a strong influence on water absorption under drought stress (Weng et al., 2000; Casmali et al., 2021).

Variation in water use among tomato plant types is therefore attributable to genotypic differences in root system development. Large root systems are often associated with improved drought tolerance in plants (Altunlu et al., 2012; Zhang et al., 2019). Consequently, the use of drought-tolerant rootstocks has been proposed as an effective strategy for enhancing drought tolerance in both fruit trees and vegetable crops (Marguerit et al., 2012; Cantero-Navarro et al., 2016).

In horticultural practice, rootstock genotypes are well recognized for their influence on scion performance, particularly in water uptake and use efficiency (Opazo et al., 2019; Liu et al., 2023). Rootstock–scion combinations also determine the capacity of scions to adapt to environmental stresses (Opazo et al., 2019; Schwarz et al., 2010). In vegetable crops, improved performance and drought tolerance can be achieved by selecting suitable rootstock and scion genotypes. Tomato rootstock genotypes, in particular, have demonstrated the potential to mitigate root-zone moisture stress in grafted plants (Zhang et al., 2019).

Within the Solanaceae family, grafting has been widely reported to enhance performance and tolerance to abiotic stresses (Rouphael et al., 2016; Dabrowski et al., 2019; Liu et al., 2023). Beyond stress mitigation, grafting also provides opportunities for quality enhancement, thereby offering a practical solution for adapting crops to environmental challenges, including drought (Schwarz et al., 2010; Liu et al., 2023). In the context of climate change, grafting with compatible rootstock–scion combinations reportedly gained wide acceptance as a viable strategy to improve productivity, quality, and tolerance to both abiotic and biotic stresses, especially in vegetables (Berdeja et al., 2015; Zhang et al., 2019).

In this study, significant interactions were observed between plant type and irrigation regime on root-zone moisture content, as well as on the growth and gas exchange of tomato. These interactions provide clear evidence of the combined influence of irrigation regime and rootstock genotype on the water relations of tomato. Notably, the highest values for these attributes were recorded in grafted plants under well-irrigated conditions, whereas the lowest values occurred in non-grafted plants exposed to soil moisture deficit.

Conclusion

Irrigation treatment and tomato plant type (non-grafted and self-grafted using rootstock and scion genotypes) significantly influenced tomato growth and physiological functions. Grafting improved tomato growth and physiological attributes—including stomatal conductance, transpiration, and photosynthetic CO_2 assimilation—across all irrigation levels. Grafted plants also exhibited enhanced water use efficiency (WUE), with both instantaneous (A/E) and intrinsic (A/gs) efficiencies increased under well-watered and wet-dry treatments. Tomato rootstock genotypes differed in growth performance, gas exchange variables, and water use efficiencies. Among the genotypes, intrinsic water use efficiency was highest in Unifort and in self-grafted plants, and lowest in Maxifort. Rootstock–scion combinations further modulated tomato growth and physiological attributes under the different irrigation conditions (well-irrigated, wet-dry, and dry-down). This study demonstrated that rootstocks influence physiological and growth parameters of tomato under variable irrigation levels, with direct implications for growth and gas exchange. The findings indicate that appropriate irrigation regimes combined with grafting strategies can be adopted to improve tomato tolerance to moisture deficit stress and to enhance water use efficiency (water-saving traits). Importantly, the study provides insights into the degree of control exerted by tomato rootstock genotypes on scion performance, particularly under variable irrigation conditions.

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Author Contributions

AS and SD contributed to the conception and design of the experiment and performed the measurements. Data analysis was carried out by AS and SD. AS conducted most of the greenhouse and laboratory activities and prepared the manuscript draft. SD, as lead author, provided insights into the experimental design, interpretation of outputs, and manuscript preparation. All authors have read and approved the final version of the manuscript.

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Conflict of Interest

The authors indicate no conflict of interest in this work.

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