



## Unlocking the Potential of Heirloom Tomatoes as Rootstocks for Sustainable Greenhouse Tomato Production

Hamdiah Eini Garsadafi<sup>a</sup>, Sadegh Mousavi-Fard<sup>b\*</sup>, Bahman Zahedi<sup>a</sup>, Abdolhossein Rezaei Nejad<sup>a</sup>

<sup>a</sup>Department of Horticultural Science, Faculty of Agriculture, Lorestan University, Khorramabad, Iran

<sup>b</sup>Department of Horticultural Science, Faculty of Agriculture, Shahrekord University, Shahrekord, Iran

Original Article

Use your device to scan and read the article online



**Citation:** Eini Garsadafi, H, Mousavi-Fard, S, Zahedi, B. and Rezaei Nejada. A. 2026. Unlocking the Potential of Heirloom Tomatoes as Rootstocks for Sustainable Greenhouse Tomato Production. Greenhouse Plant Production Journal 3(2): 18-30.

<https://doi.org/10.66224/gppj.3.2.18>

### KEYWORDS

Graft compatibility  
Landrace  
Marketable yield  
Root biomass  
Splice grafting

### ABSTRACT

Heirloom tomatoes (*Solanum lycopersicum* L.) are highly valued for their superior quality, yet their potential as rootstocks remains largely unexplored. The experiment followed a 4×2 factorial arrangement consisting of four rootstock levels (the commercial hybrid 'Parisa', two heirloom rootstocks, and a non-grafted control) and two scion cultivars ('Sylviana' and 'E15B.50115'). Under this design, grafting success, vegetative vigor, yield, and fruit quality were assessed. The commercial rootstock 'Parisa' maximized total yield, reaching 1316.93 g/plant, while the Heirloom1 rootstock achieved a competitive marketable fruit percentage of 84.28%, comparable to the commercial hybrid. Beyond these primary yield components, heirloom rootstocks significantly improved fruit quality attributes compared to non-grafted controls, specifically increasing fruit firmness, titratable acidity (up to 4.12 mL), and total soluble solids (up to 4.87 °Brix), as well as enhancing morphometric traits such as larger fruit diameter (6.31 cm) and increased pericarp thickness. These reproductive and quality benefits were supported by enhanced vegetative vigor, with Heirloom1 producing the tallest plants (279.67 cm) and the highest root dry weight (13.72 g). Consequently, these findings demonstrate that while commercial rootstocks excel in total biomass production, heirloom rootstocks provide a superior strategy for optimizing marketable quality and physiological performance in greenhouse production. These findings demonstrate that locally adapted heirloom genotypes are valuable, under-utilized genetic resources. Their use as rootstocks offers a strategy to improve plant vigor, fruit quality, and sustainability in high-value greenhouse tomato production systems.

### ARTICLE

### HISTORY

**Received:** 15 March 2026

**Revised:** 12 May 2026

**Accepted:** 28 May 2026

\* Corresponding author: S. Mousavifard  
E-mail address: [Mousavifard.s@sku.ac.ir](mailto:Mousavifard.s@sku.ac.ir)



**Abbreviations:** ANOVA, analysis of variance; CRD, completely randomized design; HR, high resistance; IR, intermediate resistance; LSD, least significant difference; ns, non-significant; TA, titratable acidity; ToCSV, tomato chlorosis virus; ToMV, tomato mosaic virus; TSWV, tomato spotted wilt virus; TSS, total soluble solids; TYLCV, tomato yellow leaf curl virus.

## 1. Introduction

Tomato (*Solanum lycopersicum* Mill.) is one of the most economically important horticultural crops worldwide and is cultivated under a wide range of production systems, from open-field cultivation to highly controlled greenhouse environments (Toni et al., 2021; Maureira et al., 2022). Beyond yield, consumer demand is increasingly focused on sensory attributes and nutritional quality, including fruit flavor, texture, and bioactive compounds. This shift in market preferences has renewed interest in heirloom tomato cultivars, which are traditionally valued for their superior organoleptic quality and rich genetic diversity (Ortiz and Dwivedi, 2025).

Heirloom tomatoes represent genetically diverse, open-pollinated populations that have evolved through farmer selection and local adaptation. Their high intra- and inter-population variability is associated with unique fruit sensory profiles, but also with susceptibility to biotic and abiotic stresses and inconsistent yield performance (Burato et al., 2025). In contrast, modern commercial hybrids are bred for uniformity, disease resistance, and postharvest performance, often at the expense of flavor quality. This trade-off between productivity and sensory quality has become a central challenge for sustainable tomato production systems, particularly under the increasing environmental constraints imposed by climate change on Mediterranean greenhouse horticulture (Fanourakis et al., 2025b).

Grafting creates an immediate physical union between two genotypes and can transfer desirable traits to farms and gardens more rapidly than conventional hybridization, which requires repeated cycles of breeding, selection, and balancing root, shoot, and fruit characteristics. Vegetable grafting has therefore emerged as a promising strategy for combining the favorable traits of traditional and modern cultivars through beneficial rootstock–scion interactions. By uniting a vigorous or stress-tolerant rootstock with a high-quality scion, grafting enhances crop productivity, nutrient assimilation, and environmental resilience (Ingram et al., 2022). While numerous studies confirm that grafting improves tomato yield and vegetative vigor, its impact on fruit quality remains inconsistent. These effects appear to be governed by the genetic compatibility between the scion and rootstock, alongside environmental factors that dictate the organoleptic properties and shelf-life potential of greenhouse vegetables (Fanourakis et al., 2025a).

Despite the expanding literature on tomato grafting, most studies focus on commercial hybrid rootstocks, whereas little attention has been paid to the potential of heirloom genotypes as rootstocks. Heirloom tomatoes possess unique physiological traits, extensive root system plasticity, and high genetic diversity, which may provide novel opportunities to modulate scion performance (Dwivedi et al., 2019). Nevertheless, the physiological interactions between heirloom rootstocks and modern greenhouse scions, particularly with respect to fruit quality, yield components, and vegetative growth, remain poorly understood (Arthur et al., 2021).

Therefore, the present study aimed to evaluate the effects of two heirloom tomato genotypes and one commercial hybrid rootstock on vegetative growth, yield, and fruit quality traits of two greenhouse scion cultivars under controlled conditions. By systematically assessing graft-take success, plant vigor, fruit morphometric characteristics, yield components, and quality parameters, this work seeks to elucidate whether heirloom rootstocks can serve as viable alternatives to commercial rootstocks and contribute to the production of high-quality tomatoes with improved agronomic performance. Beyond assessing heirloom genotypes merely as functional substitutes for commercial hybrids, this study positions heirloom tomatoes as a novel breeding reservoir for rootstock development by providing untapped genetic resources to enhance fruit quality and physiological adaptability in future greenhouse production systems.

## 2. Materials and methods

### 2.1. Experimental design and plant material

The greenhouse experiment was conducted at the Department of Horticulture, Faculty of Agriculture, Lorestan University, Khorramabad, Iran (33°29' N, 48°22' E). The site is situated at an elevation of 1148 m above sea level. The region characterized by a semi-arid continental climate, with recorded minimum and maximum air temperatures of -14.6 °C and 47 °C, respectively, and a mean annual precipitation of approximately 499 mm.

The experiment was arranged as a factorial based on a completely randomized design (CRD). Experimental units were randomly assigned to greenhouse positions using a random number generator to avoid spatial bias. The two factors included three rootstock genotypes and two greenhouse tomato cultivars used as scions.

The characteristics of all cultivars are presented in (Table 1). Five tomato cultivars were evaluated, comprising two greenhouse cultivars ('Sylviana' and 'E15B.50115') used as scions, one commercial hybrid ('Parisa'), and

two heirloom cultivars ('Heirloom1' and 'Heirloom2') used as rootstocks. The heirloom rootstock seedlings were developed from local landraces originally collected in Kermanshah, Iran.

The selected cultivars represent contrasting genetic backgrounds and production purposes, allowing a comprehensive evaluation of rootstock–scion interactions. The commercial hybrids 'Sylviana' and 'E15B.50115' were chosen as scions because they are widely used greenhouse cultivars characterized by high productivity, uniform fruit quality, and resistance to major tomato pathogens. The hybrid rootstock 'Parisa' was included as a reference standard due to its established use in commercial grafting systems and documented vigor and disease resistance. In contrast, the two heirloom genotypes (Table. 1) were selected to explore the potential of locally adapted landraces as alternative rootstocks, given their genetic diversity, robust vegetative growth, and presumed tolerance to environmental constraints typical of western Iran. This combination enabled direct comparison between commercial and heirloom rootstocks in terms of graft compatibility, plant vigor, yield formation, and fruit quality responses.

## 2.2. Plant culture, grafting, and experimental layout

Rootstock and scion seeds were sown in seedling trays. Seed quality was considered critical for achieving uniform germination and seedling development, as variation in seed vigor strongly affects stem diameter and graft compatibility. After emergence (Seven to ten days after sown, the seeds began to germination) and initial growth, seedlings were transplanted into plastic pots (10 cm top diameter × 8 cm height). Simultaneously, non-grafted scions were sown to serve as control plants. Seedlings were grown in a soil mixture consisting of equal parts (1:1:1, v/v/v) of animal manure, fine sand, and garden soil. Seedlings were grown in a soil mixture consisting of equal parts (1:1:1, v/v/v) of animal manure, fine sand, and garden soil. The physico-chemical analysis of this combined growth medium showed a loam texture with a pH of 7.4 and an electrical conductivity (EC) of 1.1 dS m<sup>-1</sup>. Due to the inclusion of organic manure, the medium was characterized by an organic carbon content of 1.6%, total nitrogen (N) of 0.11%, available phosphorus (P) of 48.5 ppm, and available potassium (K) of 425 ppm. Tomato seedlings reached the ideal stage for grafting approximately 21 to 28 days after sowing (DAS), characterized by the development of three to four true leaves and a stem diameter suitable for the procedure.

Splice grafting was employed, as it is widely used in solanaceous crops and is characterized by simplicity, rapid healing, and high success rates in tomato (Pardo-Alonso et al., 2020). Rootstock and scion seedlings with similar stem diameters were selected. The rootstock was cut a few centimeters above the soil surface, and both rootstock and scion were cut at a 45° angle. The scion was aligned with the rootstock to ensure proper contact of the vascular cambium, and the graft union was secured using plastic clips or grafting tape (Fig. 1).

To create a high-humidity healing chamber, a 30-cm wire was bent into an arch and inserted into the pot, and a transparent plastic bag was placed over the frame (Fig. 1). A small amount of water was sprayed daily inside the bag to maintain high humidity, and a small hole was made to allow limited ventilation. Grafted seedlings were transferred to a controlled environment, where graft union formation typically occurred within 7–10 days.

Post-grafting conditions were maintained at >95% relative humidity and at 27–29 °C to promote callus formation and vascular reconnection. After successful union formation, seedlings were gradually acclimatized to ambient conditions. The period from grafting to completion of hardening lasted more than three weeks. Grafting clips were left in place until they naturally detached. Before transplanting, graft success was evaluated by recording the number of successful and failed grafts, and the graft-take percentage was calculated.

The experimental field was divided into four rows, each assigned to one rootstock genotype, with the fourth row consisting of non-grafted control plants. Each row was subdivided into two sections planted with either 'E15B.50115' or 'Sylviana' scions. Each section contained 18 plants spaced 30 cm apart, with 1 m alleys between rows. Each experimental unit consisted of six plants, and the experiment was conducted with three replications. In total, 108 grafted tomato plants were grown (3 rootstocks × 2 scions × 6 plants × 3 replications), and 36 non-grafted plants were included as controls.

## 2.3. Greenhouse control and growing conditions

After bed preparation, seedlings were transplanted into the greenhouse soil two days after pre-irrigation. Planting holes approximately 10 cm deep were prepared, and grafted plants were positioned so that the graft union remained above the soil surface. Plant spacing was 30 cm, and drip irrigation was applied immediately after transplanting.

A drip irrigation system was installed with one emitter located 5 cm from each plant. During early growth, irrigation was applied every two days for 1 h and later adjusted to once every three days for 1.5 h.

Greenhouse temperature was maintained at approximately 25 °C during the day and 18 °C at night, with relative humidity controlled between 65 and 70%. Ventilation was achieved using exhaust fans and adjustable vents.

Plants were trained to a single stem using overhead wires positioned at 2.3 m height and supported with 2.5-m plastic strings. To promote early vegetative growth, all flowers, fruits, and lateral shoots were removed up to 30 cm from the plant base. Thereafter, only lateral shoots were removed, and senescent leaves were periodically pruned (Fig. 1).

The leafminer (*Liriomyza* spp.) was managed using an Integrated Pest Management (IPM) approach, including manual removal of infested leaves and yellow sticky traps. Chemical control was conducted using imidacloprid (Confidor 35% SC) at a rate of 0.35 mL L<sup>-1</sup> (applied twice at a 10-day interval during the early vegetative stage) and chlorfenapyr (Supercraf 240 g L<sup>-1</sup> SC) at a rate of 0.5 mL L<sup>-1</sup> during the peak infestation period. Additionally, soil fertility was enhanced by incorporating 8–10 kg m<sup>-2</sup> of farmyard manure prior to transplanting.

## 2.4. Traits evaluated and measurement methods

The evaluated traits were classified into fruit quality traits and plant growth and yield traits.

Fruit length and diameter were measured on three fruits per replicate using a digital caliper, and mean values were calculated. Pedicel length was measured after fruit detachment using a digital caliper. Fruit firmness was determined at the red-ripe stage using a penetrometer fitted with an 8-mm probe. Seed content was evaluated by extracting, washing, oven-drying, and weighing seeds from three fruits per replicate. Pericarp thickness was measured at the equatorial region using a digital caliper.

Total soluble solids (TSS) were determined using a handheld refractometer (Atago, Japan) after calibration with distilled water, and values were expressed as °Brix. Titratable acidity (TA) was measured by titrating fruit juice with 0.1 N NaOH and expressed as percentage of citric acid (Kabaş et al., 2024). Juice pH was measured using a calibrated pH meter.

Plant height was measured at the end of the harvest period on three plants per experimental unit. The number of flower clusters and the number of flowers per inflorescence were recorded weekly throughout the growing period. Roots were washed and weighed to determine fresh root weight and then oven-dried at 75 °C for 48 h to determine dry weight. Root length was measured from crown to tip after washing.

Leaf area was determined by scanning six leaves per replicate and analyzing the images using Image Tools software. Stem diameter, scion diameter, and graft union diameter were measured using a digital caliper at 1 cm above and below the graft union. Shoot biomass was determined by harvesting shoots at crown level and recording their fresh weight at the end of the experiment.

Fruit clusters were counted weekly, and fruit set percentage was calculated per inflorescence. Harvesting began on 5 August, and fruits were collected, counted, and weighed at each harvest to calculate total yield per plant. Individual fruit weight was recorded throughout the harvest period.

Harvested fruits were categorized based on their appearance and weight. Fruits weighing less than 50 g or showing deformities were classified as second-grade. The marketable fruit percentage was determined by calculating the number of marketable fruits as a percentage of the total number of fruits harvested per plant.

## 2.5. Statistical Analysis

All data were analyzed using SAS software (version 9.0; SAS Institute, Cary, NC, USA). Analysis of variance (ANOVA) was performed according to the factorial CRD. Mean comparisons were conducted using the least significant difference (LSD) test at the 5% probability level ( $P \leq 0.05$ ). Graphs were generated using Excel.

## 3. Results

### 3.1. Effect of Rootstocks on Grafting Success Rate

The splice grafting method resulted in high overall graft success, with significant differences in graft-take percentage among rootstocks. The highest graft-take was recorded for the commercial hybrid rootstock ‘Parisa’ (Fig. 2).

Although initial graft-take percentages were high across all treatments, clear differences emerged after transplanting. Plants grafted onto ‘Parisa’ maintained the highest post-transplant survival rate, whereas those grafted onto heirloom rootstocks exhibited a moderate decline in survival relative to their initial graft-take percentages (Fig. 2).



Fig. 1. Experimental layout illustrating the stages of: (A) tomato seed sowing, (B) seedling production, (C) chamber, (D) acclimatization under plastic humidity conditions to enhance graft-take ratio, (E) transplantation of grafted seedlings into the greenhouse soil, (F) grafting union, and (G), (H) fruits produced by grafting.

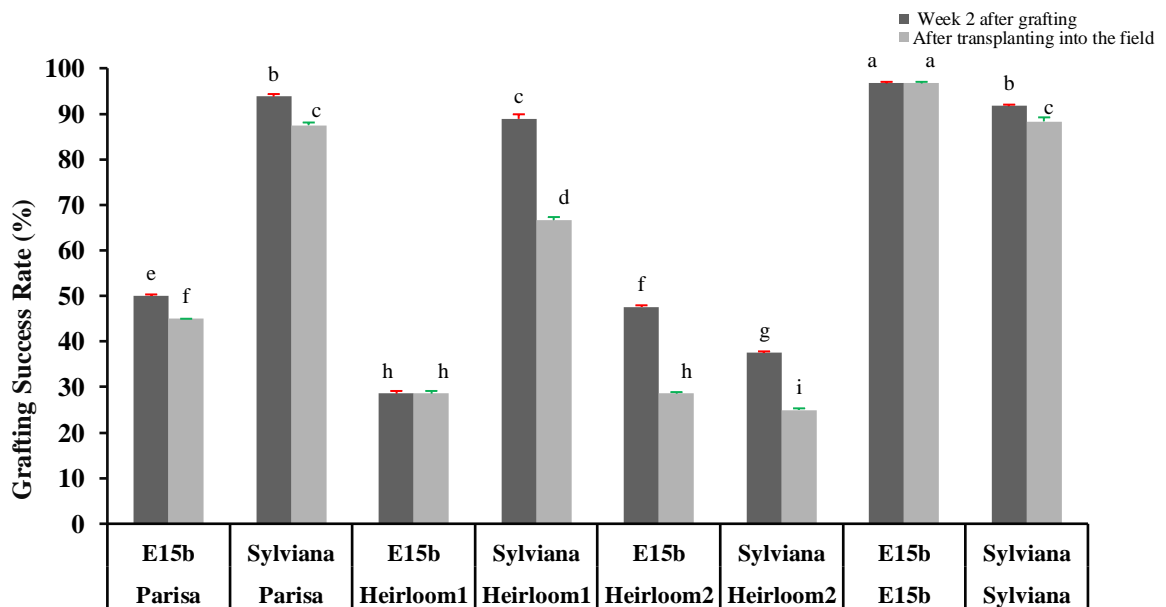







Fig. 2. graft-take percentage and final survival rate of grafted tomato plants measured two weeks after grafting and after transplanting to the greenhouse

**Table 1. Origin, biological characteristics, and intended role (scion or rootstock) of the tomato cultivars used in the experiment. HR, high resistance; IR, intermediate resistance; ToCSV, tomato chlorosis virus; ToMV, tomato mosaic virus; TSWV, tomato spotted wilt virus; TYLCV, tomato yellow leaf curl virus.**

Cultivar	Type /Role/ Growth habit	Breeding origin	Main use / Production system	Fruit characteristics	Disease resistance / tolerance
 Parisa	F1 hybrid - rootstock- Indeterminate	Sakata Seed Southern Africa	Greenhouse, plastic tunnels, shade-net houses	Uniform fruit size and shape, high fruit quality	HR: <i>Fusarium</i> wilt races 1–2, <i>Verticillium</i> wilt (Vd:1), leaf mold races 1–2, ToMV; IR: TYLCV, ToCSV, TSWV
 Sylvian a	F1 hybrid - scion- Indeterminate	Enza Zaden (The Netherlands), origin South Africa	Long-cycle greenhouse production	Round, deep-red fruits	HR: ToMV (0–2), <i>Fusarium</i> races A–C, <i>Verticillium</i> (Vd:0, Fol:0–2); IR: TYLCV, TSWV, root-knot nematodes
 E15B.5 0115	F1 hybrid - scion- Indeterminate	Enza Zaden (The Netherlands)	Greenhouse production	Medium to large fruits, uniform shape	Resistant to <i>Fusarium</i> wilt races 1–2, <i>Verticillium</i> wilt, root-knot nematodes
 Heirloom m1	Open-pollinated heirloom - rootstock- Indeterminate	Local landrace, Kermanshah (Iran)	Traditional and greenhouse cultivation	Large fruits, excellent flavor, long fruiting period	High tolerance to <i>Fusarium oxysporum</i> and <i>Verticillium dahliae</i> .
 Heirloom m2	Open-pollinated heirloom cherry - rootstock- Indeterminate	Local landrace, Kermanshah (Iran)	Traditional, breeding material	Cherry-type fruits, mild acidity, excellent flavor	Tolerant to local environmental and biotic stresses

**Table 2. Analysis of variance (ANOVA) for the effects of rootstock, scion, and their interaction on qualitative fruit characteristics of tomato.** ns, \*, and \*\* denote non-significant and significant effects at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively. TA, titratable acidity; TSS, total soluble solids.

Source of variation	D F	Mean of squares								
		Fruit Firmness	Pedice l	Seed Conten	Fruit Diamete	Fruit length	pH	TSS (Brix°)	TA	Pericarp Thicknes
Rootstock	3	2.975**	2.819**	0.062**	0.752*	0.554*	0.024 <sup>ns</sup>	1.330**	3.482*	5.299**
Scion	1	1.293*	2.7**	0.084**	4.242**	1.804*	0.493*	0.150	1.707*	1.643*
Rootstock	3	0.060 <sup>ns</sup>	0.067 <sup>ns</sup>	0.008*	0.097 <sup>ns</sup>	0.028	0.014 <sup>ns</sup>	0.164	0.370*	0.352 <sup>ns</sup>
Error	16	0.392	0.586	0.002	0.188	0.177	0.013	0.117	0.059	0.563
CV (%)		10.41	8.66	15.42	7.4	8.43	2.81	1.7	7.08	3.59

**Table 3. Effects of rootstock on qualitative fruit characteristics of tomato.** Means followed by different letters are significantly different at  $P \leq 0.05$  according to the LSD test. TA, titratable acidity; TSS, total soluble solids.

	Treatment	Fruit length (cm)	Fruit Diameter (cm)	Seed Content (g)	Pedicle Length (mm)	Fruit Firmness (N)	pH	TSS (Brix°)	TA (mL)	Pericarp Thickness (mm)
Rootstock	Parisa	4.94 <sup>ab</sup>	5.9 <sup>ab</sup>	0.33 <sup>a</sup>	9.05 <sup>a</sup>	6.07 <sup>a</sup>	4.01 <sup>a</sup>	4.87 <sup>a</sup>	3.9 <sup>a</sup>	8.96 <sup>a</sup>
	Heirloom1	5.33 <sup>a</sup>	6.31 <sup>a</sup>	0.37 <sup>a</sup>	9.26 <sup>a</sup>	6.31 <sup>a</sup>	3.97 <sup>a</sup>	4.62 <sup>ab</sup>	4.12 <sup>a</sup>	8.25 <sup>ab</sup>
	Heirloom2	5.07 <sup>ab</sup>	5.76 <sup>b</sup>	0.32 <sup>a</sup>	9.2 <sup>a</sup>	6.65 <sup>a</sup>	4.08 <sup>a</sup>	4.4 <sup>b</sup>	3.28 <sup>b</sup>	7.44 <sup>bc</sup>
	Control	4.6 <sup>b</sup>	5.45 <sup>b</sup>	0.14 <sup>b</sup>	7.8 <sup>b</sup>	5.02 <sup>b</sup>	4.11 <sup>a</sup>	3.77 <sup>c</sup>	2.42 <sup>c</sup>	6.81 <sup>c</sup>
Scion	E15b	5.26 <sup>a</sup>	6.27 <sup>a</sup>	0.35 <sup>a</sup>	9.17 <sup>a</sup>	5.78 <sup>a</sup>	3.9 <sup>b</sup>	4.3 <sup>a</sup>	3.69 <sup>a</sup>	8.13 <sup>a</sup>
	Sylvania	4.60 <sup>b</sup>	5.43 <sup>b</sup>	0.23 <sup>ab</sup>	8.49 <sup>b</sup>	6.24 <sup>a</sup>	4.19 <sup>a</sup>	4.49 <sup>a</sup>	3.16 <sup>b</sup>	7.6 <sup>a</sup>

### 3.2. Fruit length, fruit diameter, pedicel length, and fruit firmness

According to the analysis of variance (Table 2), rootstock significantly affected fruit length at  $P \leq 0.05$ . The Heirloom1 rootstock produced the longest fruits (5.33 cm), whereas the shortest fruits were recorded in the non-grafted *Sylviana* control (4.6 cm) (Table 3). Scion also had a highly significant effect ( $P \leq 0.01$ ), with 'E15B.50115' producing longer fruits than 'Sylviana', while the rootstock  $\times$  scion interaction was not significant (Table 2).

Fruit diameter was significantly influenced by rootstock at  $P \leq 0.05$  (Table 2). Heirloom1 produced the largest fruit diameter (6.31 cm), whereas Heirloom2 did not differ from the control (Table 3). Scion had a significant effect at  $P \leq 0.01$ , with 'E15B.50115' producing larger fruits than 'Sylviana', while no significant interaction was observed (Table 2).

Both rootstock and scion significantly affected pedicel length at  $P \leq 0.01$  (Table 2). The longest pedicels were recorded in fruits from the Heirloom1 rootstock (9.26 mm), which did not differ significantly from Heirloom2 and Parisa, while the shortest pedicels were observed in the control (7.8 mm) (Table 3). No significant interaction between rootstock and scion was detected (Table 2).

Rootstock significantly affected fruit firmness ( $P \leq 0.01$ ), whereas scion also had a significant effect at  $P \leq 0.05$  (Table 2). Among rootstocks, Parisa, Heirloom1, and Heirloom2 did not differ significantly, but all produced firmer fruits than the control (Table 3). Fruits from the 'Sylviana' scion exhibited the highest firmness, although they were not significantly different from those of 'E15B.50115'.

### 3.3. Seed content, pericarp thickness, total soluble solids, titratable acidity, and pH

Seed content was significantly influenced by rootstock, scion, and their interaction (Table 2). The highest seed content was observed in fruits of the 'E15B.50115' scion grafted onto Heirloom1, followed by Heirloom2, whereas the lowest value occurred in the non-grafted *Sylviana* control (Table 3).

Rootstock significantly affected pericarp thickness at  $P \leq 0.01$ , whereas no significant rootstock  $\times$  scion interaction was detected (Table 2). The Parisa rootstock produced the thickest pericarp (8.96 mm), while the control produced the thinnest (6.81 mm) (Table 3). Scion also had a significant effect, although mean comparisons revealed no clear differences between scions (Table 3).

TSS were significantly affected by rootstock at  $P \leq 0.01$  (Table 2). The highest TSS value was recorded in fruits grafted onto Parisa (4.87 °Brix), whereas the lowest value occurred in the non-grafted control (3.77 °Brix) (Table 3).

TA was significantly affected by rootstock, scion, and their interaction ( $P \leq 0.05$ ) (Table 2). The highest acidity was recorded in the 'E15B.50115' scion grafted onto Heirloom1 (4.12 mL), while the lowest value occurred in the non-grafted *Sylviana* control (2.35 mL) (Table 3). Overall, fruits of 'E15B.50115' had significantly higher TA than those of 'Sylviana' (Table 3).

Fruit pH was not affected by rootstock or the interaction between factors, but was significantly influenced by scion at  $P \leq 0.01$  (Table 2), with higher pH values observed in fruits of the 'Sylviana' scion (Table 3).

### 3.4. Plant height, number of flower clusters, and number of flowers per inflorescence

Rootstock significantly affected plant height ( $P \leq 0.01$ ), whereas the rootstock  $\times$  scion interaction was not significant (Table 4). The tallest plants were obtained with the Heirloom1 rootstock (279.67 cm), followed by Heirloom2 (274.50 cm), while the control (249.30 cm) and Parisa (242.50 cm) did not differ significantly (Table 5).

Both rootstock and scion significantly affected the number of flower clusters per plant ( $P \leq 0.01$ ), and their interaction was also significant ( $P \leq 0.05$ ) (Table 4). The highest number of flower clusters (14.3) was observed in the combination of Heirloom1 rootstock and *Sylviana* scion, whereas the lowest number was recorded in the non-grafted control (Table 5).

The number of flowers per inflorescence was significantly influenced by scion ( $P \leq 0.01$ ) and rootstock ( $P \leq 0.05$ ), whereas their interaction was not significant (Table 4). The *Sylviana* scion produced the highest number of flowers per inflorescence (Table 5).

### 3.5. Fresh and dry root weight, root length, and shoot fresh weight

Fresh root weight was significantly affected by rootstock and by the rootstock  $\times$  scion interaction ( $P \leq 0.01$ ) (Table 4). The highest fresh root weight was recorded in the Heirloom1  $\times$  *Sylviana* combination (43.3 g), while the lowest value occurred in the Parisa  $\times$  E15B.50115 combination (25.44 g) (Table 6).

**Table 4. Analysis of variance (ANOVA) for the effects of rootstock, scion, and their interaction on quantitative growth traits of tomato plants.** ns, \*, and \*\* denote non-significant and significant effects at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively.

Source of variation	D F	Mean of squares										
		Scion Diameter	Graft Union Diam	Shoot Fresh Weig	Stem Diameter	Leaf Area	Root Len	Dry Root Weigh	Fresh Root Weig	Num. of Flowers Per	Num. of Flow	Plant Height
Rootstock	3	10.06	20.54	289827	9.344*	96.4	21.8	32.855*	173.2	1.453*	34.39	2016.11*
Scion	1	1.904*	0.516*	367537	0.479 <sup>n</sup>	72.8	3.37	3.056*	0.561 <sup>n</sup>	2.667**	24**	66.67 <sup>ns</sup>
Rootstock*	3	0.896 <sup>n</sup>	0.223 <sup>n</sup>	111489	1.037 <sup>n</sup>	32.6	6.81	7.880 <sup>ns</sup>	119.1	0.084 <sup>ns</sup>	8.89*	158.78 <sup>ns</sup>
Error	1	0.496	0.163	41024.	0.911	42.4	20.2	1.995	18.31	0.513	2.75	223.29
CV (%)		5.64	2.15	15.73	7.66	11.9	12.1	13.32	12.58	16.03	18.59	5.7

**Table 5. Effects of rootstock on quantitative growth traits of tomato plants.** Means followed by different letters are significantly different at  $P \leq 0.05$  according to the LSD test.

Treatment	Shoot Fresh Weight (g)	Graft Union Diameter (mm)	Scion Diameter (mm)	Stem Diameter (mm)	Dry Root Weight (g)	Fresh Root Weight (g)	Num. of Flowers Per	Num. of Flow	Plant Height (cm)
Rootstock									
Parisa	989 <sup>b</sup>	19.8 <sup>a</sup>	11.89 <sup>c</sup>	11.83 <sup>b</sup>	10.99 <sup>b</sup>	31.41 <sup>b</sup>	4.76 <sup>a</sup>	9.3 <sup>b</sup>	242.5 <sup>b</sup>
Heirloom	1496.67 <sup>a</sup>	19.8 <sup>a</sup>	14.03 <sup>a</sup>	13.78 <sup>a</sup>	13.72 <sup>a</sup>	42.06 <sup>a</sup>	4.93 <sup>a</sup>	14.3 <sup>a</sup>	279.67 <sup>a</sup>
Heirloom	1395.33 <sup>a</sup>	19.39 <sup>a</sup>	12.95 <sup>b</sup>	13.18 <sup>a</sup>	9.14 <sup>c</sup>	31.65 <sup>b</sup>	4.3 <sup>ab</sup>	8 <sup>bc</sup>	274.5 <sup>a</sup>
Control	1266.67 <sup>a</sup>	15.98 <sup>b</sup>	11.04 <sup>c</sup>	11.04 <sup>b</sup>	8.5 <sup>c</sup>	30.9 <sup>b</sup>	3.83 <sup>b</sup>	6.3 <sup>c</sup>	249.3 <sup>b</sup>
Scion									
E15b	1410.67 <sup>a</sup>	18.89 <sup>a</sup>	12.76 <sup>a</sup>	12.59 <sup>a</sup>	10.23 <sup>a</sup>	33.8 <sup>a</sup>	4.13 <sup>b</sup>	7.91 <sup>b</sup>	259.83 <sup>a</sup>
Sylviana	1163.17 <sup>b</sup>	18.59 <sup>a</sup>	12.19 <sup>a</sup>	12.32 <sup>a</sup>	10.94 <sup>a</sup>	34.6 <sup>a</sup>	4.8 <sup>a</sup>	9.92 <sup>a</sup>	263.17 <sup>a</sup>

Rootstock had a significant effect on root dry weight ( $P \leq 0.01$ ), whereas the interaction with scion was not significant (Table 4). Heirloom1 produced the highest root dry weight (13.72 g), followed by Parisa (10.99 g), whereas Heirloom2 did not differ significantly from the control (Table 5). Scion also had a significant effect ( $P \leq 0.05$ ), although no clear differences were detected between scions.

### 3.6. Root length was not significantly affected by rootstock, scion, or their interaction.

Both rootstock and scion significantly influenced shoot fresh weight ( $P \leq 0.01$ ), and their interaction was also significant ( $P \leq 0.05$ ) (Tables 4). The highest shoot biomass (1774 g) was recorded in plants grafted onto Heirloom1 with the E15B.50115 scion, whereas the lowest value (936 g) was observed in the Parisa  $\times$  E15B.50115 combination (Table 6).

### 3.7. Leaf area, stem diameter, scion diameter, and graft union diameter

Leaf area was not significantly affected by rootstock, scion, or their interaction (Table 4).

Stem diameter was significantly affected by rootstock ( $P \leq 0.01$ ) (Table 4). The largest stem diameter was observed in Heirloom1 (13.78 mm), followed by Heirloom2 (13.18 mm), whereas the control and Parisa had significantly smaller diameters (Table 5). Scion and the rootstock  $\times$  scion interaction had no significant effect (Table 4).

Scion diameter was also significantly influenced by rootstock ( $P \leq 0.01$ ), with Heirloom1 producing the thickest scions (14.03 mm), while the control exhibited the smallest diameter (11.04 mm) (Table 5).

Graft union diameter was significantly affected by both rootstock ( $P \leq 0.01$ ) and scion ( $P \leq 0.05$ ), whereas their interaction was not significant (Table 4). The Parisa, Heirloom1, and Heirloom2 rootstocks produced the greatest graft union diameters, with no significant differences among them (Table 5).

### 3.8. Number of fruit clusters, fruit set percentage, and ratio of marketable fruits

Rootstock, scion, and their interaction had no significant effect on the number of fruit clusters per plant (Table 7). Rootstock significantly affected the percentage of marketable fruits ( $P \leq 0.05$ ) (Table 7). The highest proportion of marketable fruits was recorded for the Heirloom1 rootstock (84.28%), which did not differ significantly from Parisa (82.25%) (Table 8). Scion also had a highly significant effect ( $P \leq 0.01$ ), with the 'E15B.50115' scion producing a higher percentage of marketable fruits than 'Sylviana', whereas the rootstock  $\times$  scion interaction was not significant (Table 7).

### 3.9. Fruit weight and total yield per plant

Fruit weight was significantly affected by rootstock, scion, and their interaction ( $P \leq 0.01$ ) (Table 7). The highest fruit weight (127.93 g) was recorded in the combination of Heirloom2 rootstock with the 'E15B.50115' scion, which did not differ significantly from the Heirloom1 and Parisa rootstocks grafted with the same scion (Table 6). Fruits from plants grafted with 'Sylviana' were consistently lighter, with the lowest value observed in the non-grafted Sylviana control (65.91 g) (Table 6).

Total fruit yield per plant was significantly influenced by both rootstock and scion ( $P \leq 0.01$ ), whereas their interaction was not significant (Table 7). The highest yield was obtained with the Parisa rootstock (1316.93 g), while the control treatment produced the lowest yield (690 g) (Table 8). Among scions, 'Sylviana' yielded more (1101 g) than 'E15B.50115' (943.78 g) (Table 8).

**Table 6. Interaction effects of rootstock and scion on single fruit weight, seed content, titratable acidity (TA), shoot fresh weight, and number of flower clusters of tomato.** Means followed by different letters are significantly different at  $P \leq 0.05$  according to the LSD test.

Rootstock	Scion	Fresh Root Weight	Seed Content (gr)	TA (mL)	Shoot Fresh Weight (g)	Num. of Flower Cluster	Fruit weight (g)
<b>Rootstock* Scion</b>							
Parisa	E15b	25.44 <sup>e</sup>	0.37 <sup>ab</sup>	4.17 <sup>b</sup>	936 <sup>d</sup>	7.67 <sup>cd</sup>	116.82 <sup>a</sup>
	Sylviana	37.37 <sup>ab</sup>	0.286 <sup>bc</sup>	3.63 <sup>c</sup>	1042 <sup>cd</sup>	11 <sup>b</sup>	69.99 <sup>c</sup>
Heirloom1	E15b	40.8 <sup>ab</sup>	0.43 <sup>a</sup>	4.73 <sup>a</sup>	1774 <sup>a</sup>	9.66 <sup>bc</sup>	122.103 <sup>a</sup>
	Sylviana	43.3 <sup>a</sup>	0.31 <sup>b</sup>	3.5 <sup>cd</sup>	1219.33 <sup>bcd</sup>	14.3 <sup>a</sup>	82.69 <sup>b</sup>
Heirloom2	E15b	34.3 <sup>bcd</sup>	0.43 <sup>a</sup>	3.4 <sup>cd</sup>	1548.67 <sup>ab</sup>	7.67 <sup>cd</sup>	127.93 <sup>a</sup>
	Sylviana	29 <sup>cde</sup>	0.21 <sup>cd</sup>	3.17 <sup>d</sup>	1242 <sup>bcd</sup>	8.33 <sup>bcd</sup>	85.37 <sup>b</sup>
Non-Grafted	Control	34.86 <sup>bc</sup>	0.167 <sup>de</sup>	2.48 <sup>e</sup>	1384 <sup>bc</sup>	6.67 <sup>d</sup>	91.03 <sup>b</sup>
	Control	26.98 <sup>de</sup>	0.114 <sup>c</sup>	2.35 <sup>e</sup>	1149.33 <sup>cd</sup>	6 <sup>d</sup>	65.91 <sup>c</sup>

**Table 7. Analysis of variance (ANOVA) for the effects of rootstock, scion, and their interaction on yield components and the ratio of marketable to second-grade tomato fruits.** ns, \*, and \*\* denote non-significant and significant effects at  $P \leq 0.05$  and  $P \leq 0.01$ , respectively.

Source of Variation	DF	Mean of squares				
		Total yield per plant (g)	Fruit weight (g)	The ratio of marketable fruit to second-grade fruit (%)	Fruit set (%)	Number of fruit cluster
Rootstock	3	396812.975 <sup>**</sup>	932.021 <sup>**</sup>	342.49 <sup>*</sup>	123.272 <sup>ns</sup>	1.389 <sup>ns</sup>
Scion	1	149847.681 <sup>**</sup>	8884.994 <sup>**</sup>	670.98 <sup>**</sup>	158.466 <sup>ns</sup>	0.667 <sup>ns</sup>
Rootstock*	3	10187.025 <sup>ns</sup>	132.831 <sup>**</sup>	11.91 <sup>ns</sup>	78.853 <sup>ns</sup>	0.556 <sup>ns</sup>
Error	16	9548.627	43.677	108.04	194.579	1.375
CV (%)		9.55	6.94	13.23	17.72	27.59

**Table 8. Effects of rootstock on yield components and the ratio of marketable to second-grade tomato fruits.** Means followed by different letters are significantly different at  $P \leq 0.05$  according to the LSD test.

		Total yield per plant (g)	Fruit weight (g)	The ratio of marketable fruit to second-grade fruit (%)
Rootstock	Parisa	1316.93 <sup>a</sup>	93.41 <sup>b</sup>	82.25 <sup>a</sup>
	Heirloom1	1056.11 <sup>b</sup>	102.39 <sup>a</sup>	84.28 <sup>a</sup>
	Heirloom2	1028.17 <sup>b</sup>	106.65 <sup>a</sup>	73.18 <sup>ab</sup>
	Control	690 <sup>c</sup>	84.7 <sup>c</sup>	68.28 <sup>b</sup>
Scion	E15b	943.78 <sup>b</sup>	114.47 <sup>a</sup>	82.28 <sup>b</sup>
	Sylviana	1101.82 <sup>a</sup>	75.99 <sup>b</sup>	71.71 <sup>b</sup>

## 4. Discussion

### 4.1. Grafting success and compatibility of heirloom rootstocks

The high graft-take percentages observed in the present study confirm the suitability of the splice grafting method for tomato and are consistent with previous reports describing its high success in solanaceous crops (Pardo-

Alonso et al., 2019; Chandanshive et al., 2023). The superior graft success recorded for the commercial hybrid rootstock 'Parisa' (Fig. 2) likely reflects its uniform seedling growth, genetic stability, and breeding for graft compatibility. In contrast, the reduced graft-take observed with heirloom rootstocks, particularly when combined with the 'E15B.50115' scion (Fig. 2), may be attributed to greater variability in stem diameter, anatomical mismatches, and physiological incompatibility typical of open-pollinated landraces. The observed divergence between graft union formation and post-transplant survival suggests that anatomical compatibility alone is insufficient for successful field establishment. Beyond the initial callus formation, physiological stress tolerance during the transplanting phase, likely mediated by root hydraulic conductivity, wound healing efficiency, and early root regeneration capacity, plays a critical role in the successful establishment of grafted plants in greenhouse environments.

Despite their lower graft success, heirloom rootstocks exhibited excellent post-transplant performance, as reflected by their enhanced vegetative growth and biomass accumulation (Tables 4 and 5), Frey et al. (2021) suggested that graft union formation rather than long-term functional compatibility represents the principal limitation of their use. These findings emphasize that graft compatibility screening is essential when heirloom germplasm is introduced into grafting programs (Babar et al., 2023).

#### 4.2. Influence of heirloom rootstocks on vegetative vigor

Heirloom1 and Heirloom2 significantly enhanced plant height, stem diameter, scion diameter, and shoot biomass compared with the commercial hybrid and non-grafted controls (Tables 4 and 5). These results demonstrate that locally adapted heirloom genotypes can function as highly vigorous rootstocks (Lang and Nair, 2019). Enhanced vegetative growth is commonly attributed to improved water and nutrient uptake capacity and to the upward translocation of root-derived hormones such as cytokinins and gibberellins (Kappel et al., 2024).

The superior root biomass and dry root weight observed in plants grafted onto Heirloom1 (Table 5) indicate a more extensive and physiologically active root system. Similar responses have been reported by Bristow et al. (2021) in tomato and other vegetable crops, where vigorous rootstocks enhance shoot growth, leaf expansion, and canopy development through improved root hydraulic conductivity and mineral acquisition.

#### 4.3. Rootstock–scion interactions and reproductive development

The significant increase in the number of flower clusters and flowers per inflorescence in grafted plants, particularly in the Heirloom1 × Sylviana combination, highlights the strong regulatory role of the rootstock on reproductive sink formation. The presence of significant rootstock × scion interactions for these traits (Tables 6), Mauro (2022) confirms that the expression of reproductive performance depends on genetic compatibility rather than rootstock vigor alone.

These responses likely reflect differences in carbohydrate partitioning, hormonal balance, and long-distance signaling between scion and rootstock, supporting the concept that grafting represents a dynamic physiological integration rather than a simple additive process (Lu et al., 2020; Akhiyarova et al., 2024).

The interaction patterns observed for flower cluster number and shoot biomass can be attributed to differences in source–sink balance and hormonal cross-talk between the graft partners. Rootstocks vary in their capacity to export cytokinins, auxins, and abscisic acid, which regulate meristem activity, inflorescence initiation, and assimilate partitioning (Martínez-Andújar et al., 2016).

In addition, Xie et al. (2019) reported that the efficiency of vascular reconnection at the graft union influences phloem transport and xylem hydraulic continuity, thereby modulating carbon allocation to developing reproductive sinks. Collectively, these mechanisms determine whether grafted plants prioritize vegetative growth or reproductive output, explaining the genotype-specific interaction patterns observed in the present study.

#### 4.4. Effects on fruit size, yield, and marketability

Fruit length, diameter, and single fruit weight were significantly enhanced by grafting (Tables 3 and 8), with the largest fruits obtained from heirloom rootstocks. Heirloom1 consistently produced larger fruit size and greater shoot biomass (Tables 3 and 5), whereas Parisa maximized total yield per plant (Table 8). These contrasting responses indicate that heirloom rootstocks favor individual fruit development, whereas commercial hybrids are more effective at maximizing overall productivity, this observation is supported by the results from other studies (Gong et al., 2022).

The percentage of marketable fruits recorded for Heirloom1 did not differ significantly from the commercial cultivar Parisa (Table 8). Our results stand in contrast to the findings of Lang and Nair (2019), where significant yield quality gaps were identified between heirloom and commercial types. These discrepancies might be attributed to differences in local environmental conditions or the specific scion–rootstock combinations evaluated in the

present. Improvements in marketability are likely associated with enhanced fruit firmness and pericarp thickness (Table 3), contributing to improved fruit uniformity (Walubengo et al., 2022; Nie et al., 2024; Kayikci et al., 2026).

#### 4.5. Rootstock effects on fruit quality attributes

Grafting significantly affected fruit firmness, TSS, TA, pericarp thickness, and seed content (Tables 2 and 3) (Dorin et al., 2019; Hashem et al., 2024). Rootstock-mediated modulation of fruit firmness, soluble solids, and TA observed in the present study is consistent with the concept that preharvest physiological regulation strongly determines postharvest quality potential in greenhouse vegetables, with tomato exhibiting pronounced sensitivity to root-zone and canopy-level drivers (Fanourakis et al., 2025a). Dodgson et al. (2023) reported that increased firmness and pericarp thickness may result from altered calcium transport, enhanced cell wall biosynthesis, and modified fruit water relations, all of which are regulated by rootstock genotype (Table 3). Similar improvements in firmness and delayed softening have been linked to enhanced calcium availability and modulation of antioxidant and cell wall-degrading enzymes following preharvest nutritional management in sweet pepper (Moosavi-Nezhad et al., 2024).

Higher TSS and TA values in fruits grafted onto Parisa and Heirloom1 indicate that rootstocks modulate primary and secondary metabolism in the scion (Table 3). These effects are likely mediated by improved assimilate transport efficiency and regulation of sugar–acid balance (Zhou et al., 2022; Cai et al., 2025). Parisi et al. (2023) demonstrated that the strong rootstock  $\times$  scion interaction for seed content and TA further confirms the specificity of long-distance physiological signaling (Table 6). Changes in fruit firmness and soluble solids observed in grafted plants may also have important implications for postharvest hydration status and storability, which can now be assessed non-destructively using visible-light imaging combined with machine-learning approaches (Makraki et al., 2025). This demonstrates that rootstock choice is not only a preharvest decision but also a key determinant of postharvest performance potential.

#### 4.6. Implications for the use of heirloom germplasm in grafting systems

The identification of locally adapted heirloom rootstocks with high vigor and improved fruit quality is significant for preserving genetic diversity. These native resources provide a robust genetic base that could be further evaluated in future breeding programs for environmental resilience (Fanourakis et al., 2025b). Importantly, the present findings suggest that heirloom tomatoes should not be regarded merely as alternatives to commercial hybrids, but rather as a new breeding reservoir for the development of climate-smart rootstocks tailored to future greenhouse production challenges (Fullana-Pericas et al., 2020). This study demonstrates that heirloom tomato genotypes possess substantial potential as alternative rootstocks. Their capacity to enhance vegetative growth, fruit size, seed content, firmness, and marketable yield (Tables 3 and 8) (Fullana-Pericas et al., 2020; Gioia et al., 2010) highlights the importance of conserving and exploiting local landraces within sustainable horticultural systems (Grieneisen et al., 2018).

However, the lower graft-take percentages observed in heirloom combinations (Fig. 2) represent a practical limitation. This constraint should be addressed through optimized seedling synchronization, anatomical screening, and selection for graft compatibility traits. Long-term evaluation under stress conditions is also required to assess their resilience and economic feasibility (Loupit and Cookson., 2020; DuVal et al., 2025).

#### 4.7. Limitations and future research directions

The experiment was conducted during a single growing season in one greenhouse environment; therefore, multi-year and multi-location trials are necessary to confirm the stability of the observed responses across growth, yield, and fruit quality traits (Tables 3, 5, and 8). Only two heirloom genotypes were evaluated as rootstocks, and wider screening of landrace germplasm is needed to validate the generality of the effects reported here.

Moreover, physiological mechanisms such as root hydraulic conductivity, mineral uptake efficiency, hormonal regulation, and assimilate partitioning were not examined, although they likely underlie the observed differences in vegetative vigor and fruit quality (Tables 3 and 5). Graft union anatomy and compatibility, which may explain the lower graft-take rates of heirloom combinations (Fig. 2), also warrant detailed histological investigation.

Finally, postharvest behavior and sensory quality were not evaluated, despite the clear rootstock effects on fruit firmness, TSS, and TA (Tables 3 and 5). Integrating multi-environment validation, physiological and anatomical analyses, and postharvest quality assessments will be essential for fully exploiting heirloom tomatoes as rootstocks in sustainable greenhouse production systems.

### Conclusions

This study demonstrates that heirloom tomato genotypes are not merely traditional varieties but highly effective biological tools for optimizing greenhouse production. From a practical management perspective, the results indicate that rootstock selection should be driven by specific production goals: while commercial hybrids like

'Parisa' are ideal for maximizing total biomass and yield, native genotypes, specifically Heirloom1, offer a superior strategic advantage for growers targeting premium markets. Due to its native adaptation and high environmental compatibility, Heirloom1 significantly enhanced fruit physical characteristics, achieving the highest individual fruit weight across all treatments and improving pericarp thickness and fruit firmness.

Furthermore, the observed rootstock–scion interactions provide a practical guideline for greenhouse operators: grafting success is a genotype-specific synergy, meaning that compatibility must be trialed for specific scion–rootstock pairs rather than assuming success based on rootstock vigor alone. The ability of Heirloom1 to maintain a high marketable fruit percentage (84.28%) while simultaneously elevating chemical quality (TSS and TA) demonstrates its tangible economic value in high-value or niche markets where quality directly correlates with profitability. In conclusion, integrating locally adapted heirloom germplasm into grafting programs provides a resilient and cost-effective pathway to bridge the gap between high productivity and superior fruit quality in sustainable greenhouse systems.

## Acknowledgement

The authors thank the research greenhouse staff at Lorestan University for their technical assistance.

## Author Contributions

H.E.G. conducted the study, performed experiments, collected the data, and contributed to writing the initial draft of the manuscript. S.M.F. defined and supervised the project, managed administration and funding acquisition, contributed to conceptualization and methodology, performed statistical analyses after data collection, and edited the initial draft. B.Z. defined and supervised the project and funding acquisition. A.R.N. contributed to writing the initial draft as well as reviewing and editing the manuscript. All authors have read and approved the final version of the manuscript.

## Funding

This research received no external funding.

## Conflict of Interest

The authors indicate no conflict of interest in this work.

## References

- Akhiyarova, G., Finkina, E.I., Zhang, K., Veselov, D., Vafina, G., Ovchinnikova, T.V. and Kudoyarova, G., 2024. The long-distance transport of some plant hormones and possible involvement of lipid-binding and transfer proteins in hormonal transport. *Cells*, 13(5), p.364. <https://doi.org/10.3390/cells13050364>
- Arthur, J.D., Li, T., Lalk, G.T. and Bi, G., 2021. High tunnel production of containerized hybrid and heirloom tomatoes using grafted plants with two types of rootstocks. *Horticulturae*, 7(9), p.319. <https://doi.org/10.3390/horticulturae7090319>
- Babar, M., Afzal, N., Siddiqui, K., Azhar, A. and Galani, S., 2023. Exploring graft incompatibility markers: Intraspecific and interspecific grafts of tomato (*Solanum lycopersicum* L.). *Scientia Horticulturae*, 310, p.111762. <https://doi.org/10.1016/j.scienta.2023.111762>
- Bristow, S.T., Hernandez-Espinoza, L.H., Bonarota, M.S. and Barrios-Masias, F.H., 2021. Tomato rootstocks mediate plant-water relations and leaf nutrient profiles of a common scion under suboptimal soil temperatures. *Frontiers in plant science*, 11, p.618488. <https://doi.org/10.3389/fpls.2020.618488>
- Burato, A., Tava, A., Biazzi, E., Parisi, M., Tripodi, P., Scalzo, R.L., Bianchi, G., Picchi, V. and Ronga, D., 2025. Changes in processing tomato fruit quality in heirloom and modern varieties developed over the past decades. *Journal of Food Composition and Analysis*, 146, p.107956. <https://doi.org/10.1016/j.jfca.2025.107956>
- Cai, H., Liang, M., Qin, X., Dong, R., Wang, X., Wang, H., Sun, S., Cui, X., Yang, W. and Li, R., 2025. Tonoplast sugar transporters coordinately regulate tomato fruit development and quality. *Plant Communications*, 6(5).
- Chandanshive, A., Sonavane, P., Gaikwad, S., & Kumar, V. 2023. Response of tomato (*Solanum lycopersicum*) grafted on wild brinjal (*Solanum torvum*) rootstock for growth and yield. *The Indian Journal of Agricultural Sciences*, 93, 881–887.
- Dodgson, J., Weston, A.K. and Marks, D.J., 2023. Tomato firmness and shelf-life increased by application of stimulated calcium. *Crops*, 3(4), pp.251–265. <https://doi.org/10.3390/crops3040023>
- Dorin, S.O.R.A., Doltu, M., Drăghici, E.M. and Bogoescu, M.I., 2019. Effect of grafting on tomato fruit quality. *Notulae Botanicae Horti Agrobotanici Cluj-Napoca*, 47(4), pp.1246–1251. <https://doi.org/10.15835/nbha47411719>

- DuVal, A.E., Tempeleu, A., Schmidt, J.E., Puig, A., Knollenberg, B.J., Chaparro, J.X., Stevens, M.E. and Motamayor, J.C., 2025. Evidence of Graft Incompatibility and Rootstock Scion Interactions in Cacao. *Horticulturae*, 11(8), p.899. <https://doi.org/10.3390/horticulturae11080899>
- Dwivedi, S., Goldman, I. and Ortiz, R., 2019. Pursuing the potential of heirloom cultivars to improve adaptation, nutritional, and culinary features of food crops. *Agronomy*, 9(8), p.441. <https://doi.org/10.3390/agronomy9080441>
- Fanourakis, D., Makraki, T., Spyrou, G.P., Karavidas, I., Tsaniklidis, G. and Ntatsi, G., 2025a. Environmental Drivers of Fruit Quality and Shelf Life in Greenhouse Vegetables: Species-Specific Insights. *Agronomy*, 16(1), p.48. <https://doi.org/10.3390/agronomy16010048>
- Fanourakis, D., Tsaniklidis, G., Makraki, T., Nikoloudakis, N., Bartzanas, T., Sabatino, L., Fatnassi, H. and Ntatsi, G., 2025. Climate Change Impacts on Greenhouse Horticulture in the Mediterranean Basin: Challenges and Adaptation Strategies. *Plants*, 14(21), p.3390. <https://doi.org/10.3390/plants14213390>
- Frey, C., Álvarez, R., Encina, A. and Acebes, J.L., 2021. Tomato graft union failure is associated with alterations in tissue development and the onset of cell wall defense responses. *Agronomy*, 11(6), p.1197. <https://doi.org/10.3390/agronomy11061197>
- Fullana-Pericàs, M., Conesa, M.À., Ribas-Carbó, M. and Galmés, J., 2020. The use of a tomato landrace as rootstock improves the response of commercial tomato under water deficit conditions. *Agronomy*, 10(5), p.748. <https://doi.org/10.3390/agronomy10050748>
- Gioia, F.D., Serio, F., Buttarò, D., Ayala, O. and Santamaria, P., 2010. Influence of rootstock on vegetative growth, fruit yield and quality in 'Cuore di Bue', an heirloom tomato. *The Journal of Horticultural Science and Biotechnology*, 85(6), pp.477-482. <https://doi.org/10.1080/14620316.2010.11512701>
- Gong, T., Brecht, J.K., Koch, K.E., Hutton, S.F. and Zhao, X., 2022. A systematic assessment of how rootstock growth characteristics impact grafted tomato plant biomass, resource partitioning, yield, and fruit mineral composition. *Frontiers in Plant Science*, 13, p.948656. <https://doi.org/10.3389/fpls.2022.948656>
- Grieneisen, M.L., Aegerter, B.J., Scott Stoddard, C. and Zhang, M., 2018. Yield and fruit quality of grafted tomatoes, and their potential for soil fumigant use reduction. A meta-analysis: Yield and fruit quality of grafted tomatoes, and their potential for soil fumigant use reduction. A meta-analysis. *Agronomy for Sustainable Development*, 38(3), p.29. <https://doi.org/10.1007/s13593-018-0507-5>
- Hashem, A., Bayoumi, Y., El-Zawily, A.E.S., Tester, M. and Rakha, M., 2024. Interspecific hybrid rootstocks improve productivity of tomato grown under high-temperature stress. *HortScience*, 59(1), pp.129-137. <https://doi.org/10.21273/HORTSCII7482-23>
- Ingram, T.W., Sharpe, S., Trandel, M., Perkins-Veazie, P., Louws, F.J. and Meadows, I., 2022. Vigorous rootstocks improve yields and increase fruit sizes in grafted fresh market tomatoes. *Frontiers in Horticulture*, 1, p.1091342. <https://doi.org/10.3389/fhort.2022.1091342>
- Kabaş, A., Ercan, U., Kabas, O. and Moiceanu, G., 2024. Prediction of total soluble solids content using tomato characteristics: comparison artificial neural network vs. multiple linear regression. *Applied Sciences*, 14(17), p.7741. <https://doi.org/10.3390/app14177741>
- Kappel, N., Palla, B., Challa, L. and Mozafarian, M., 2024. Rootstock and scion anatomical parameters in grafted eggplant seedlings, influencing growth and fruit production. *BMC Plant Biology*, 24(1), p.1207. <https://doi.org/10.1186/s12870-024-05926-4>
- Kayikci, H.C., Aydin, S., Adak, A., Dogan, A., Sapkota, M., Feng, Q. and Topcu, Y., 2026. Association mapping of tomato fruit quality for weight, firmness, brix, and color using GWAS. *BMC Plant Biology*. 26, 41. <https://doi.org/10.1186/s12870-025-07838-3>
- Lang, K.M. and Nair, A., 2019. Effect of tomato rootstock on hybrid and heirloom tomato performance in a midwest high tunnel production system. *HortScience*, 54(5), pp.840-845. <https://doi.org/10.21273/HORTSCII3874-19>
- Loupit, G. and Cookson, S.J., 2020. Identifying molecular markers of successful graft union formation and compatibility. *Frontiers in Plant Science*, 11, p.610352. <https://doi.org/10.3389/fpls.2020.610352>
- Lu, X., Liu, W., Wang, T., Zhang, J., Li, X. and Zhang, W., 2020. Systemic long-distance signaling and communication between rootstock and scion in grafted vegetables. *Frontiers in Plant Science*, 11, p.460. <https://doi.org/10.3389/fpls.2020.00460>
- Makraki, T., Tsaniklidis, G., Papadimitriou, D.M., Taheri-Garavand, A. and Fanourakis, D., 2025. Non-Destructive monitoring of postharvest hydration in cucumber fruit using Visible-Light color analysis and Machine-Learning models. *Horticulturae*, 11(11), p.1283.
- Martínez-Andújar, C., Albacete, A., Martínez-Pérez, A., Pérez-Pérez, J.M., Asins, M.J. and Pérez-Alfocea, F., 2016. Root-to-shoot hormonal communication in contrasting rootstocks suggests an important role for the ethylene precursor aminocyclopropane-1-carboxylic acid in mediating plant growth under low-potassium nutrition in tomato. *Frontiers in plant science*, 7, p.1782. <https://doi.org/10.3389/fpls.2016.01782>
- Maureira, F., Rajagopalan, K. and Stöckle, C.O., 2022. Evaluating tomato production in open-field and high-tech greenhouse systems. *Journal of Cleaner Production*, 337, p.130459.

- Mauro, R.P., Pérez-Alfocea, F., Cookson, S.J., Ollat, N. and Vitale, A., 2022. Physiological and molecular aspects of plant rootstock-scion interactions. *Frontiers in Plant Science*, 13, p.852518. <https://doi.org/10.3389/fpls.2022.852518>
- Moosavi-Nezhad, M., Homayonzadeh, M., Tsaniklidis, G., Roessner, U., Woltering, E.J., Fanourakis, D. and Aliniaiefard, S., 2024. Enhancing shelf life of bell peppers through preharvest fertigation with calcium and potassium thiosulfate: A focus on antioxidant and cell wall degradation enzymes. *Journal of Agriculture and Food Research*, 17, p.101262.
- Nie, H., Yang, X., Zheng, S. and Hou, L., 2024. Gene-based developments in improving quality of tomato: focus on firmness, shelf life, and pre-and post-harvest stress adaptations. *Horticulturae*, 10(6), p.641. <https://doi.org/10.3390/horticulturae10060641>
- Ortiz, R. and Dwivedi, S.L., 2025. Profiling Heirloom Tomato Germplasm: Metabolites, Textural Traits, and Consumer Preferences. In *Next Generation Food Crops for Human Health* (pp. 213-221). CRC Press.
- Pardo-Alonso, J.L., Carreño-Ortega, Á., Martínez-Gaitán, C.C. and Fatnassi, H., 2020. Behavior of different grafting strategies using automated technology for splice grafting technique. *Applied Sciences*, 10(8), p.2745.
- Pardo-Alonso, J.L., Carreño-Ortega, Á., Martínez-Gaitán, C.C., Golasi, I. and Gómez Galán, M., 2019. Conventional industrial robotics applied to the process of tomato grafting using the splicing technique. *Agronomy*, 9(12), p.880. <https://doi.org/10.3390/agronomy9120880>
- Parisi, M., Pentangelo, A., D'Alessandro, A., Festa, G., Francese, G., Navarro, A., Sanajà, V.O. and Mennella, G., 2023. Grafting effects on bioactive compounds, chemical and agronomic traits of 'Corbarino' tomato grown under greenhouse healthy conditions. *Horticultural Plant Journal*, 9(2), pp.273-284. <https://doi.org/10.1016/j.hpj.2022.03.001>
- Toni, H.C., Djossa, B.A., Ayenan, M.A.T. and Teka, O., 2021. Tomato (*Solanum lycopersicum*) pollinators and their effect on fruit set and quality. *The Journal of Horticultural Science and Biotechnology*, 96(1), pp.1-13.
- Walubengo, D., Orina, I., Kubo, Y. and Owino, W., 2022. Physico-chemical and postharvest quality characteristics of intra and interspecific grafted tomato fruits. *Journal of Agriculture and Food Research*, 7, p.100261.
- Xie, L., Dong, C. and Shang, Q., 2019. Gene co-expression network analysis reveals pathways associated with graft healing by asymmetric profiling in tomato. *BMC plant biology*, 19(1), p.373. <https://doi.org/10.1186/s12870-019-1976-7>
- Zhou, Z., Yuan, Y., Wang, K., Wang, H., Huang, J., Yu, H. and Cui, X., 2022. Rootstock-scion interactions affect fruit flavor in grafted tomato. *Horticultural Plant Journal*, 8(4), pp.499-510. <https://doi.org/10.1016/j.hpj.2022.01.001>