

Article

Comparative Drought Response of *Solanum melongena*, *S. macrocarpon*, *S. dasyphyllum*, and *S. melongena* × *S. dasyphyllum* Interspecific Hybrids

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Abstract

Drought stress is a major constraint in eggplant cultivation, limiting growth, physiological performance and yield. *Solanum* relatives may provide alleles for improving drought tolerance. The objective of this study was to evaluate the responses of cultivated, wild and interspecific eggplant genotypes under water stress to identify drought-tolerant genotypes. Four-week-old plants of three Greek eggplant cultivars—*S. macrocarpon* (cultivated), *S. dasyphyllum* (wild), and three *S. melongena* × *S. dasyphyllum* hybrids—were grown under full and deficit irrigation and assessed for 10 agronomic and 7 physiological traits. Genotype, irrigation level and their interaction significantly affected most traits. Eggplant showed greater sensitivity under water stress with reductions in 9 agronomical traits, such as leaf number (12.9–15.8%), plant height (15.4–25.1%), LAI (47.7–55.4%), root (32.1–46.6%) and plant biomass (31.4–38.6%). *S. dasyphyllum* and *S. macrocarpon* maintained relative growth and physiological stability through different mechanisms, indicating enhanced drought tolerance. *S. dasyphyllum* exhibited reduction only in leaf number (11.5%), plant height (17.8) and LAI (23.9%), while *S. macrocarpon* exhibited reduction only in leaf length (18.1%) and LAI (55.0%). Interspecific hybrids displayed intermediate responses and heterosis under control (−22.2 to 66.6%) and stress (−29.8 to 81.5%) conditions. These findings support the use of wild or cultivated germplasm in breeding drought-resilient eggplant cultivars and rootstocks and enhancing crop sustainability.

Keywords: drought tolerance; plant breeding; crop wild relatives; interspecific hybridization; heterosis; *Solanum dasyphyllum*; *Solanum macrocarpon*



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1. Introduction

Eggplant (*Solanum melongena* L.) is a major vegetable crop of global importance, cultivated extensively in tropical and subtropical regions, particularly in Asia, the Mediterranean basin, and Africa. According to the Food and Agriculture Organization (FAO), more than 90.0% of eggplant cultivated area and production is concentrated in Asia, while some African and European countries also contribute to world production [1]. Eggplant is valued for its nutritional and economic significance but also for its adaptability to diverse agro-climatic conditions [2,3]. However, the sustainability of eggplant production is increasingly threatened by abiotic stresses, with drought being one of the most critical constraints, especially in the context of climate change [4,5].

Drought stress has significant adverse effects on eggplant growth, physiology, and yield. Reduced water availability leads to decreases in plant height, leaf number, leaf area, and overall biomass, as well as lower fruit yield and quality [6,7]. Physiologically, drought stress impairs photosynthesis, quantum yield and stomatal conductance; disrupts water and nutrient uptake; and can increase the accumulation of osmoprotectants such as proline and soluble sugars as a stress response [8–10].

The sensitivity of eggplant to drought necessitates the development of drought-resilient genotypes and the implementation of effective management strategies. Some agronomic practices, such as deficit irrigation, grafting onto drought-tolerant rootstocks, use of microbial biostimulants, and foliar nanoparticle application, have been utilized to enhance drought resilience in eggplant [11–15]. However, the incorporation of drought tolerance via plant breeding in the cultivated genotypes is always desirable in order to minimize plant care and external inputs.

In eggplant, breeding has mainly focused on enhancing yield, fruit quality and pest resistance [16–20]. However, improvement of resilience to environmental stresses is limited, underscoring the need to exploit other germplasm sources [2,6,21,22]. Wild *Solanum* species have evolved across diverse and often harsh environments, have a wide natural distribution, and frequently possess traits associated with biotic and abiotic stresses [23–28].

Interspecific hybridization between eggplant and several cultivated and wild relatives is possible and is considered a valuable strategy to broaden the genetic base of the crop and introgress beneficial alleles [29–33]. For example, eggplant introgression lines (ILs) derived from *S. tomentosum* are promising materials for the development of cultivars resistant or tolerant to nematodes, *Fusarium*, and *Verticillium* wilts [34]. Additionally, *S. incanum* and *S. insanum* have been utilized as donors for salinity and heat and drought tolerance, respectively [35,36]. Moreover, ILs and advanced backcross populations derived from *S. incanum*, *S. insanum*, *S. dasyphyllum* and *S. elaeagnifolium* facilitated the identification of quantitative trait loci (QTLs) linked to improved nutrient uptake and drought tolerance [28,31,37,38].

From another perspective, the interspecific hybrids between eggplant and its wild relatives have been successfully utilized as rootstocks, offering agronomic advantages [39–43]. Such hybrids often show transgressive performance under drought stress, often surpassing their parental lines in traits such as root biomass, water use efficiency, and biochemical resilience [44]. In this context, the development of drought-tolerant interspecific rootstocks represents a promising and rapid alternative for enhancing drought adaptation of elite eggplant cultivars. Nevertheless, the agronomical and physiological responses of eggplant interspecific hybrids under drought conditions, especially in the seedling stage, remain underexplored, and a deeper understanding of these responses could inform both breeding strategies and agronomic management practices [45].

Of particular interest for eggplant breeding are two African *Solanum* species, i.e., *S. macrocarpon* L. and *S. dasyphyllum* Schumacher & Thonn, belonging to the secondary eggplant gene pool. These species are known to possess several agronomic traits, including tolerance to water stress [45,46]. *S. macrocarpon* (gboma eggplant) is cultivated especially in Africa and is considered to have originated from the domestication of *S. dasyphyllum*. The crossability of these species to eggplant varies across studies, but the consensus is that *S. dasyphyllum* is more compatible with eggplant than *S. macrocarpon* [47].

The objective of this study was to assess the drought responses of three Greek eggplant cultivars, the African *Solanum* species *S. dasyphyllum* and *S. macrocarpon*, and three *S. melongena* × *S. dasyphyllum* interspecific hybrids at an early stage (4 weeks old) to identify drought-resilient genotypes for eggplant breeding. To achieve this, the plant material was evaluated under full and deficit irrigation regimes, based on a set of agronomic and physiological traits.

2. Materials and Methods

2.1. Plant Material

The plant material consisted of three Greek eggplant (*S. melongena* L.) cultivars, Emi (E), Langada (L), and Tsakoniki (T); the wild species *S. dasyphyllum* Schumach. & Thonn.; and their corresponding interspecific F₁ hybrids (E × Sd, L × Sd, and T × Sd). Additionally, the water-stress-tolerant *S. macrocarpon* was also included in the study. The selection of cultivated eggplant genotypes was based on their popularity, different morphological features, and frequent use in breeding programs and experimental trials. Seeds of the cultivated genotypes were obtained from the Institute of Plant Breeding and Genetic Resources (IPBGR) of ELGO-DEMETER (Thermi, Greece), while seeds of *S. dasyphyllum* and *S. macrocarpon* were obtained from the *Solanum* species collection maintained at the same institute. The interspecific hybrids were previously developed by the first author by crossing the eggplant cultivars (used as female parents) with *S. dasyphyllum*. Hybrid identity was confirmed based on morphological traits, such as the presence of spines.

2.2. Experimental Site and Conditions

The experiment was conducted during June of 2024 in greenhouse facilities at ELGO-DEMETER, Greece (latitude: 40.54° N, longitude: 22.99° E, altitude: 2 m). The climatic conditions during the experiment are shown in Figure 1. Seedlings of the plant material were raised in seedling trays filled with a fertilized peat-based substrate (TS2, Klasmann–Deilmann) and maintained under greenhouse conditions until two weeks old. At this stage, seedlings were transplanted into 0.5 L plastic pots filled with the same substrate and allowed to acclimate for an additional two weeks.

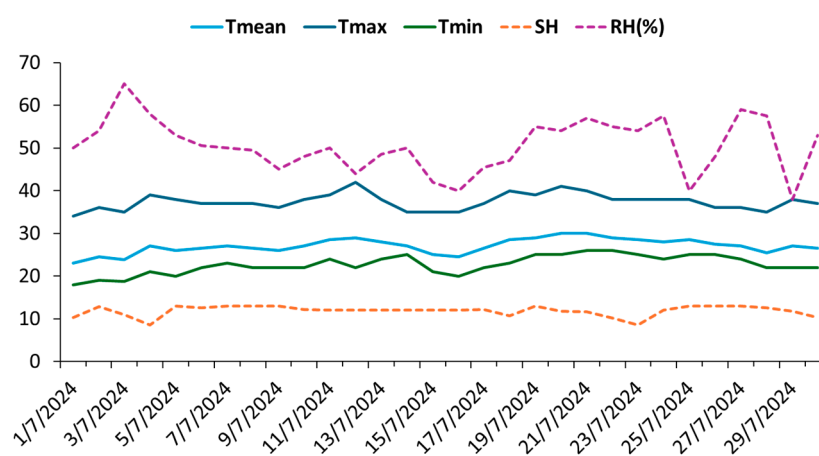


Figure 1. Climatic conditions during the experimental period. Daily minimum (Tmin), mean (Tmean), and maximum (Tmax) temperatures (in °C) in the greenhouse, together with sunshine hours (SH) and mean relative humidity (RH%), representing conditions outside the greenhouse.

2.3. Experimental Design and Irrigation Treatments

The experiment followed a factorial randomized complete block design (RCBD) with three replications, evaluating the effects of genotype and irrigation level. Each replication included all genotypes under two irrigation treatments: control (100% irrigation volume) and water stress (50% irrigation volume). Within each replication, four plants per genotype and irrigation level combination were grown and arranged in a row, with a distance of 12 cm between pots. Data were collected from three of the four plants, excluding one border plant. The entire experiment occupied an area of approximately 6 × 1.8 m. Figure A1 provides an overview of the experimental setup.

Prior to the experiment, the substrate field capacity (FC) was measured gravimetrically as described by Kadoglidou et al. [10], and the volumetric soil water content (VSWC) values corresponding to 100% FC and 50% FC were determined as $0.430 \text{ m}^3 \cdot \text{m}^{-3}$ and $0.215 \text{ m}^3 \cdot \text{m}^{-3}$, respectively, using a soil moisture sensor (5TE, Decagon Devices, Pullman, WA, USA).

The water deficit treatment began two weeks after transplantation and lasted for four weeks. Irrigation frequency was determined based on the eggplant control plants. Control pots were monitored daily at 1–2 h intervals from 07:30 a.m. onwards using the moisture sensor coupled to a ProCheck readout device (Decagon Devices, Pullman, WA, USA). When the substrate reached the 60% FC threshold, irrigation was applied to restore control soil moisture to 100% FC. Water-stressed plants received half of the irrigation of the control by using irrigation drippers with flow rates of $1 \text{ L} \cdot \text{h}^{-1}$ and $2 \text{ L} \cdot \text{h}^{-1}$, respectively, for the same irrigation duration.

The total irrigation volumes (pre-stress and stress period) were 3.02 L per plant for the control and 1.71 L per plant for the water stress treatment. During the stress period, the irrigation volumes received by the control and stress treatment were 2.35 L and 1.18 L, respectively. One week after the onset of the stress treatment, each plant received 0.5 g of a water-soluble 20-20-20 fertilizer.

2.4. Measurements of Agronomic Traits

At the end of the stress period, several agronomic traits were assessed (Table 1). Plant height (cm) was measured from the soil surface to the apical meristem, and stem diameter (mm) was determined at the level of the cotyledons using a digital caliper. The number of fully expanded leaves per plant was recorded, and leaf dimensions (cm) were determined by measuring the length and width of the third fully expanded leaf from the apex. Furthermore, shoot and root fresh and dry biomass (g) were evaluated. Plants were harvested, divided into shoots (including leaves) and roots, and their fresh weight was recorded immediately. Subsequently, the samples were oven-dried at 70°C for 48 h to determine dry biomass.

Table 1. Abbreviations used for agronomic and physiological traits measured in the present study.

Trait	Abbreviation	Unit
Agronomic		
Leaf length	LL	cm
Leaf width	LW	cm
Stem diameter	SD	mm
Leaf number	LN	
Plant height	PH	cm
Leaf area index	LAI	
Root dry weight	RDW	g
Shoot dry weight	SDW	g
Root-to-shoot ratio	R/S	
Plant dry weight	PDW	g
Physiological		
Water use efficiency	WUE	g L^{-1}
Leaf water potential	LWP	bar
Relative electrolyte leakage	REL	
Chlorophyll content index	CCI	
Malondialdehyde	MDA	$\mu\text{mol g}^{-1}$

Leaf area index was estimated at the end of the experiment using a non-destructive method with an AccuPAR LP-80 ceptometer (Decagon Devices, Pullman, WA, USA) [48]. For each genotype $\times$ irrigation treatment combination, plants from all three replications

were arranged side by side in three parallel rows (one per replication). Within each row, pots were spaced 5 cm apart, and the distance between adjacent rows was equal to the pot diameter. The ceptometer was positioned to the left of each row at pot level, and a reference reading was taken above the plant canopy, followed by three measurements per row. The average of the three readings was used to calculate the LAI for each treatment.

2.5. Measurements of Physiological Traits

Water use efficiency (WUE) was calculated as the ratio of total plant dry biomass (g) to the cumulative volume of water applied (L) per plant throughout the experimental period. Chlorophyll content was assessed using a portable Chlorophyll Content Meter (CCM-200, Opti-Sciences, Tyngsboro, MA, USA). Measurements were taken from the second fully expanded leaf from the top of every plant at three timepoints: 2, 3 and 4 weeks after the onset of the water treatment. At each measurement, the average of two readings per leaf was recorded.

Root membrane integrity was evaluated through relative electrolyte leakage (REL), following the protocol described by Kadoglidou et al. [49]. Briefly, at the end of the experiment (4 weeks after stress initiation), roots were rinsed thoroughly to remove soil residues. A 100 mg sample of root tissue was placed in 15 mL of deionized water with known electrical conductivity (EC) and vortexed vigorously. Samples were incubated in the dark for 24 h, and EC was measured using a 712 ConductoMeter (Metrohm, Herisau, Switzerland). Subsequently, samples were boiled at 110 °C for 20 min, and EC was measured again. REL was calculated and normalized per gram of fresh root weight using the following equation:

$$REL (\%) = \frac{\frac{EC \text{ before boiling}}{EC \text{ after boiling}} \times 100}{\text{initial root weight (g)}}$$

Leaf water potential (Ψ_{leaf}) was measured using a pressure chamber (Model SKPM 1405, Skye Instruments Ltd., Llandrindod Wells, UK), following the method of Scholander et al. [50]. Fully expanded leaves were excised and immediately placed in the chamber to prevent water loss. Pressure was gradually increased until xylem sap exuded from the cut surface of the petiole, and the balancing pressure was recorded. All measurements were conducted under stable environmental conditions to ensure consistency.

Lipid peroxidation was estimated by measuring malondialdehyde (MDA) content using the thiobarbituric acid (TBA) method described by Heath and Packer [51], with modifications according to Papadopoulou et al. [52]. Briefly, 200 mg of fresh leaf tissue were homogenized in 600 μL of 0.1% (*w/v*) trichloroacetic acid (TCA) and centrifuged at $15,000 \times g$ for 20 min at 4 °C. Then, 0.5 mL of the supernatant was mixed with 1.5 mL of 20% TCA containing 0.5% TBA. The mixture was incubated in a water bath at 95 °C for 25 min and then rapidly cooled in an ice bath. After a second centrifugation ($15,000 \times g$, 5 min, 4 °C), the absorbance of the supernatant was measured at 532 nm and corrected for nonspecific turbidity at 600 nm. The MDA concentration was calculated using an extinction coefficient of $155 \text{ mM}^{-1} \text{ cm}^{-1}$.

2.6. Mid-Parent and Better-Parent Heterosis

To evaluate the relative performance of the three interspecific hybrids in comparison to their parental lines, mid-parent heterosis (MPH) and better-parent heterosis (BPH; heterobeltiosis) were calculated for each trait under both irrigation regimes. These indices were determined using the following equations:

$$MPH (\%) = \frac{(F1 - MP)}{MP} \times 100$$

$$BPH (\%) = \frac{(F_1 - BP)}{BP} \times 100$$

where F_1 = hybrid mean, MP = mid-parent mean, and BP = better-parent mean.

To assess the significance of mid-parent heterosis (MPH) and better-parent heterosis (BPH), separate t -tests were performed for each hybrid and trait, comparing hybrid values against the respective mid-parent and better-parent values.

2.7. Statistical Analysis

Data were analyzed using analysis of variance (ANOVA) appropriate for a two-factor RCBD. Square-root transformed data was used for the analyses of leaf number and root-to-shoot ratio to meet the homogeneity of variance assumptions, while untransformed data were used for all the other traits. When significant differences were found ($p \leq 0.05$), the means were separated using Tukey's honest significant difference test. In addition to ANOVA, the relative performance of each genotype under full and deficit irrigation was expressed as a percentage change and used for comparative analysis. This approach was used to reduce potential confounding effects due to baseline trait differences among genotypes and to highlight their relative sensitivity or resilience to water stress. A change was considered significant when the mean value of a trait under full irrigation differed from that under water stress according to a t -test ($p < 0.05$). Pearson's correlation analysis was also performed separately for each irrigation level to assess trait associations under full and deficit irrigation. To better visualize the correlation structure, a network was generated using only the significant correlations ($p < 0.05$) with the online visualization platform Flourish [53]. In addition, principal component analysis was performed to identify relationships among the measured traits and to visualize the distribution of genotypes under control and water stress conditions. All analyses were conducted using SPSS v.17.0 (IBM Corp., Armonk, NY, USA), except PCA (XLSTAT, Lumivero, Denver, CO, USA).

3. Results

3.1. Main Effects and Interactions

3.1.1. Effects on Agronomic Traits

The analysis of variance revealed that genotype and irrigation level had a statistically significant effect ($p < 0.001$) on all measured agronomic traits, including leaf length, leaf width, stem diameter, leaf number, plant height, leaf area index, root dry weight, shoot dry weight, and total plant dry weight (Figure 2, Table A1). The root-to-shoot dry weight ratio was significantly affected only by genotype ($p < 0.001$), while irrigation level had no significant effect on this trait ($p = 0.944$). Significant genotype $\times$ irrigation level interactions were observed for leaf length ($p = 0.013$), stem diameter ($p = 0.042$), plant height ($p < 0.001$), leaf area index ($p = 0.028$), shoot dry weight ($p = 0.018$) and plant dry weight ($p = 0.021$), indicating that the response of these traits to water availability varied among genotypes. In contrast, traits such as leaf width, leaf number, root dry weight and root-to-shoot ratio did not show significant interaction effects.

3.1.2. Effects on Physiological Traits

Irrigation level significantly influenced water use efficiency (WUE, $p < 0.001$), leaf water potential (LWP, $p < 0.001$), relative electrolyte leakage (REL, $p < 0.002$), chlorophyll content index at 2 weeks (CCI 2 w, $p = 0.027$), and malondialdehyde (MDA, $p = 0.042$). Genotypic differences were highly significant for WUE ($p < 0.001$), CCI at all timepoints (2 w, 3 w, 4 w; $p < 0.001$), and MDA ($p < 0.001$). A significant genotype $\times$ irrigation level interaction was observed for WUE ($p = 0.003$), LWP ($p = 0.029$), CCI at 3 weeks ($p = 0.003$), and MDA ($p < 0.001$).

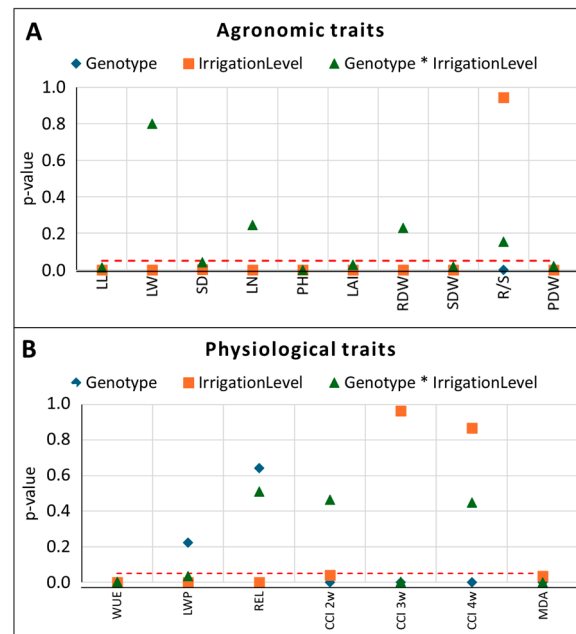


Figure 2. *p*-values from the analysis of variance (ANOVA) assessing the effects of genotype ($df = 7$), irrigation level ($df = 1$), and their interaction ($df = 7$). (A) Agronomic traits. (B) Physiological traits. The red dotted line indicates the significance threshold ($p = 0.05$).

3.2. Agronomic Traits

3.2.1. Leaf Dimensions

Under full irrigation, the longest leaves were observed in eggplant (19.1–22.1 cm) and *S. macrocarpon* (18.0 cm), whereas the shortest were in *S. dasyphyllum* (16.8 cm) (Table 2). Leaf length was significantly reduced by deficit irrigation, with reductions ranging from −12.2% in Emi to −22.6% in Tsakoniki, while Langada and *S. dasyphyllum* were not affected. Langada and Tsakoniki displayed the highest leaf length under stress (18.6 and 17.1 cm, respectively), while the lowest values were measured in TxSd (14.3 cm) and *S. dasyphyllum* (15.6 cm). Regarding leaf width, *S. dasyphyllum* and *S. macrocarpon* produced the widest leaves (11.3 and 10.8 cm, respectively) when fully irrigated, while TxSd produced the narrowest leaves (8.4 cm). Water stress reduced leaf width in most cases, notably in TxSd (−23.8%) and Langada (−23.6%). In contrast, *S. macrocarpon* and *S. dasyphyllum* showed only minor, non-significant reductions. These species maintained the widest leaves under stress (10.3 and 10.1 cm, respectively) and TxSd the narrowest (6.4 cm). Representative pairs of plants of the studied genotypes under control and water stress conditions were presented in Figure 3.

3.2.2. Stem Diameter

Stem thickness also varied among the plant materials (Table 2). Under full irrigation, the eggplant cultivars (8.7–9.8 mm) and ExSd (8.7 mm) were identified as the genotypes producing the thickest stems, whereas the thinnest stems were recorded in *S. dasyphyllum* and *S. macrocarpon* (6.8 and 6.9 mm, respectively). Water stress caused a slight reduction in stem diameter in most genotypes, with the only significant decrease observed in Langada (14.8%). Contrasting with the general trend, *S. macrocarpon* exhibited a small, non-significant increase. Eggplant Langada (8.4 mm) and *S. dasyphyllum* (6.2 mm) retained the thickest and thinnest stems, respectively, under stress.

Table 2. Agronomical and physiological traits and relative changes (%) under control and water stress (WS) conditions in eggplant cultivars Emi (E), Langada (L), and Tsakoniki (T), as well as *S. dasyphyllum* (Sd), *S. macrocarpon* (Sm), and three interspecific hybrids.

Genotype	Treatment	LL ¹	LW	SD	LN	PH	LAI	RDW	SDW	R/S	PDW	WUE	LWP	REL	CCI 2 w	CCI 3 w	CCI 4 w	MDA
E	Control	19.08 b,c	9.75 a–d	9.04 a,b	11.67 b	29.25 b,c	1.31 b,c	1.13 d,e	5.59 c,d	0.20 c,d	6.72 c,d	2.45 d	−9.17 e–g	44.91 ns	29.45 d	35.52 f–h	56.85 a–d	4.08 c–e
	WS	16.75 d,e	8.33 c,d	8.10 b–e	10.17 c,d	24.75 d	0.65 f,g	0.57 f	4.04 e,f	0.15 d	4.61 e	2.44 d	−14.67 b–d	76.90 ns	32.10 d,e	33.50 g,h	55.47 a–e	7.75 a
ExSd	Change (%)	−12.21 *	−14.56 *	−10.4 ns	−12.85 *	−15.38 *	−50.38 *	−49.56 *	−27.73 *	−25.0 ns	−31.4 *	−0.41 ns	−59.98 *	71.23 *	9.00 ns	−5.69 ns	−2.43 ns	89.95 *
	Control	18.83 b–d	10.58 a	8.71 b,c	13.50 a	28.42 b,c	1.98 a	1.75 a	7.07 a,b	0.25 a–c	8.81 a,b	2.91 a–d	−12.17 b–f	65.40 ns	35.92 c–e	53.10 d	64.78 a	3.72 c–f
L	WS	15.92 e,f	8.40 b–d	8.22 b–e	11.33 b,c	20.83 e,f	1.37 b,c	1.05 d,e	4.64 d,e	0.22 c,d	5.68 d,e	3.33 a	−13.83 b–d	68.78 ns	36.78 b–e	46.27 d–f	56.67 a–d	3.75 c–f
	Change (%)	−15.45 *	−20.6 *	−5.63 ns	−16.07 *	−26.71 *	−30.81 *	−40.0 *	−34.28 *	−12.0 ns	−35.53 *	14.43 ns	−13.64 ns	5.17 ns	2.39 ns	−12.86 *	−12.52 ns	0.81 ns
LxSd	Control	19.50 b	10.58 a	9.84 a	11.83 b	36.83 a	1.21 b–d	1.06 d,e	6.92 a,b	0.15 d	7.98 a–c	2.64 b–d	−10.25 d–g	56.57 ns	29.33 e	48.67 d,e	47.85 d–g	4.17 c–e
	WS	18.58 b–d	8.08 d,e	8.38 b–d	9.67 d	27.58 c	0.54 g	0.72 e,f	4.60 d,e	0.16 d	5.32 d,e	3.12 a,b	−19.17 a	68.52 ns	36.10 b–e	44.12 d–h	49.30 b–f	4.09 c–e
Sd	Change (%)	−4.72 ns	−23.63 *	−14.84 *	−18.26 *	−25.12 *	−55.37 *	−32.08 *	−33.53 *	6.67	−33.33 *	18.18 ns	−87.02 *	21.12 ns	23.08 ns	−9.35 ns	3.03 ns	−1.92 ns
	Control	18.33 b–d	9.92 a–d	7.96 c–e	12.50 a,b	22.08 d–f	1.84 a	1.74 a	6.58 a–c	0.27 a–c	8.32 a,b	2.99 a–c	−11.67 c–g	56.51 ns	30.43 d,e	67.80 b	63.98 a,b	5.01 b
Sm	WS	15.75 e,f	8.08 d,e	7.66 d–g	11.33 b,c	19.25 fg	0.93 d–f	1.15 c,d	4.73 d,e	0.24 b,c	5.89 d,e	3.10 a,b	−14.50 b–d	88.40 ns	32.07 d,e	54.82 c,d	63.17 a,b,c	3.42 e,f
	Change (%)	−14.08 *	−18.55 ns	−3.77 ns	−9.36 *	−12.82 *	−49.46 *	−33.91 *	−28.12 *	−11.11 ns	−29.21 *	3.68 ns	−24.25 *	56.43 *	5.39 ns	−19.14 *	−1.27 ns	−31.74 *
T	Control	16.75 d,e	11.32 a	6.77 g,h	10.17 c,d	11.92 h	1.13 c–e	1.18 c,d	4.31 e,f	0.27 a–c	5.48 d,e	1.61 e	−12.75 b–f	60.08 ns	36.87 b–e	32.73 h	48.13 c–g	4.14 c–e
	WS	15.57 e,f	10.29 a–c	6.20 h	9.00 d,e	9.79 h	0.86 e,f	1.07 d,e	3.29 f	0.33 a	4.36 e	2.55 c,d	−15.00 b,c	73.00 ns	34.10 d,e	34.40 g,h	41.29 e–g	2.45 g
TxSd	Change (%)	−7.04 ns	−9.1 ns	−8.42 ns	−11.5 *	−17.87 *	−23.89 *	−9.32 ns	−23.49 ns	22.22 ns	−20.44 ns	58.39 *	−17.65 *	21.50 ns	−7.51 ns	5.1 ns	−14.21 ns	−40.82 *
	Control	19.75 b	10.75 a	6.92 f–h	9.00 d,e	12.83 h	1.91 a	1.27 b–d	4.36 e,f	0.28 a–c	5.63 d,e	1.86 e	−8.83 fg	63.47 ns	46.28 a,b	64.27 b,c	52.28 a–e	4.40 b,c
T	WS	16.17 e,f	10.08 a–c	7.64 d–g	8.50 e	12.08 h	0.86 e,f	1.10 d,e	4.05 e,f	0.27 a–c	5.15 e	3.02 a–c	−13.67 b–e	66.08 ns	51.33 a	82.58 a	56.75 a–d	4.29 b–d
	Change (%)	−18.13 *	−6.23 ns	10.4 ns	−5.56 ns	−5.85 ns	−54.97 *	−14.17 ns	−7.11 ns	−3.57 ns	−8.53 ns	62.37 *	−52.78 *	4.11 ns	10.91 ns	28.49 *	8.55 ns	−2.5 ns
TxSd	Control	22.08 a	10.33 a,b	8.69 b,c	11.67 b	31.33 b	1.51 b	1.63 a,b	7.52 a	0.22 c,d	9.15 a	3.03 a–c	−7.33 g	52.97 ns	40.23 b–d	36.70 f–h	33.95 g	3.99 c–e
	WS	17.08 c–e	8.00 d,e	8.35 b–d	9.83 d	24.50 d	0.79 fg	1.00 d,e	4.64 d,e	0.21 c,d	5.64 d,e	3.30 a	−16.50 a,b	59.21 ns	40.88 b–d	37.57 e–h	36.88 fg	3.15 f
TxSd	Change (%)	−22.64 *	−22.56 *	−3.8 ns	−15.77 *	−21.80 *	−47.68 *	−38.65 *	−38.3 *	−4.55 ns	−38.36 *	8.91 ns	−125.1 *	11.78 ns	1.62 ns	2.37 ns	8.63 ns	−21.05 *
	Control	17.25 c–e	8.42 b–d	7.82 c–f	13.17 a	22.33 d,e	1.88 a	1.55 a–c	6.13 b,c	0.25 a–c	7.68 b,c	2.54 c,d	−11.50 c–g	59.70 ns	34.25 d,e	44.78 d–g	46.45 d–g	5.01 b
	WS	14.25 f	6.42 e	7.32 e–g	11.75 b	17.83 g	1.34 b,c	1.08 d,e	3.67 e,f	0.32 a,b	4.75 e	3.20 a	−13.67 b–e	83.60 ns	45.62 a–c	51.00 d	57.77 a–d	3.52 d–f
	Change (%)	−17.39 *	−23.75 *	−6.39 ns	−10.78 *	−20.15 *	−28.72 *	−30.32 *	−40.13 *	28.0 ns	−38.15 *	25.98 *	−18.87 *	40.03 *	33.2 *	13.89 ns	24.37 *	−29.74 *

¹ LL, leaf length (cm); LW, leaf width (cm); SD, stem diameter (mm); LN, leaf number; PH, plant height (cm); LAI, leaf area index; RDW, root dry weight (g); SDW, shoot dry weight (g); R/S, root-to-shoot ratio; PDW, plant dry weight (g); WUE, water use efficiency (g L^{−1}); LWP, leaf water potential; REL, relative electrolyte leakage; CCI 2 w, CCI 3 w, CCI 4 w, chlorophyll content index at 2, 3 and 4 weeks; MDA, malondialdehyde content (μmol g^{−1}). Different letters within each column indicate significant differences between genotypes according to Tukey's test at $p < 0.05$. ns and * indicate, respectively, non-significant and significant differences ($p < 0.05$) between the control and water stress treatment for each genotype.

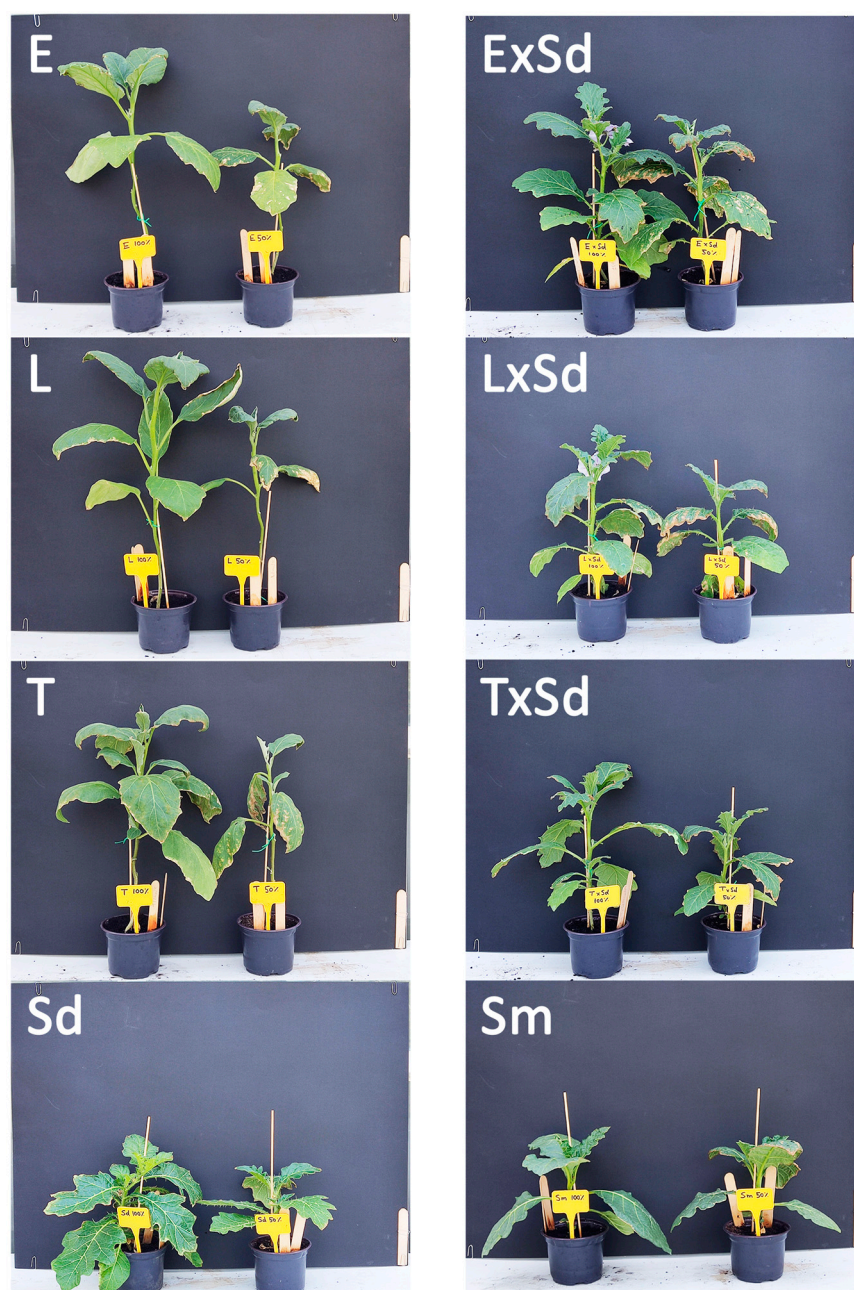


Figure 3. Representative pairs of plants of the studied genotypes. Plants grown under control (left pot) and water stress (right pot) conditions. Scale bar = 10 cm. Genotype abbreviations: Emi, Langada, Tsakoniki (*S. melongena*; E, L, T); *S. dasyphyllum* (Sd), *S. macrocarpon* (Sm).

3.2.3. Leaf Number

The interspecific hybrids consistently produced the greatest number of leaves regardless of the irrigation regime (Table 2). Under full irrigation, ExSd and TxSd formed 13.5 and 13.2 leaves, significantly surpassing the eggplant cultivars (11.7–11.8). By contrast, *S. macrocarpon* and *S. dasyphyllum* developed the fewest leaves (9.0 and 10.2, respectively). Water deficit significantly reduced leaf formation across all genotypes, apart from *S. macrocarpon*, which was not affected. The decreases ranged from −9.4% in LxSd to −18.3% in Langada. The same trend was observed under stress, as the hybrids maintained higher leaf numbers (11.3–11.8), significantly more than eggplant (9.7–10.2) and its African relatives (8.5–9.0).

3.2.4. Plant Height

Significant genotypic variation was also observed for plant height (Table 2). Fully irrigated eggplants produced taller plants (29.3–36.8 cm), while plants of *S. dasyphyllum* and *S. macrocarpon* were the shortest (11.9 and 12.8 cm, respectively). A strong negative effect of reduced irrigation was evident in all genotypes, except for *S. macrocarpon*, which was practically unaffected. The largest reduction was observed in ExSd (−26.7%) and the smallest in LxSd (−12.8%). Under deficit irrigation, eggplant cultivars still produced the tallest plants (24.5–27.6 cm), while *S. dasyphyllum* and *S. macrocarpon* were the shortest (9.8 and 12.1 cm, respectively), and the interspecific hybrids had intermediate values.

3.2.5. Leaf Area Index (LAI)

Considering the fully irrigated controls, the highest values for LAI were found in the interspecific hybrids (1.8–2.0) and *S. macrocarpon* (1.9), while the lowest was recorded in *S. dasyphyllum* (1.1) (Table 2). LAI was substantially reduced by water stress across all genotypes. The largest decreases occurred in eggplant and *S. macrocarpon* (−47.7 to −55.4%), while *S. dasyphyllum* was the least affected (−23.9%). Milder reductions were recorded in the interspecific hybrids (−28.7 to −46.5%). The highest LAI values under stress were displayed by TxSd and ExSd (1.3–1.4), while Langada had the lowest LAI value (0.5).

3.2.6. Root Dry Weight (RDW)

Analysis of biomass revealed an enhanced capacity for root allocation in the interspecific hybrids (Table 2). Under full irrigation, the highest root dry weights were recorded in ExSd and LxSd (1.8 and 1.7 g, respectively), significantly exceeding those of Emi and Langada (1.1 g each). *S. macrocarpon*, Tsakoniki, and TxSd exhibited intermediate RDW values, ranging between 1.5 and 1.6 g. Root development was limited under stress conditions, with Emi (−49.6%) and Tsakoniki (−38.7%) being the most affected genotypes. In contrast, root biomass was not affected in *S. dasyphyllum* and *S. macrocarpon*. Under stress, root dry weight ranged from 0.6 g in Emi to 1.2 g in LxSd. Representative roots of the studied genotypes under control and water stress conditions were presented in Figure 4.

3.2.7. Shoot Dry Weight (SDW)

Shoot biomass accumulation was generally enhanced in eggplant and its interspecific hybrids under full irrigation (Table 2). Tsakoniki, ExSd, Langada and LxSd had the highest shoot dry weight (6.6–7.5 g), whereas *S. dasyphyllum* and *S. macrocarpon* recorded the lowest values (4.3–4.4 g). Deficit irrigation caused a significant reduction in SDW, ranging from −27.7 to −38.3% in eggplant and from −28.1 to −40.1% in the interspecific hybrids. *S. macrocarpon* and *S. dasyphyllum* were less sensitive to stress, as indicated by minimal non-significant reductions. Under stress, *S. dasyphyllum* had the lowest SDW (3.3 g), while the rest of the genotypes ranged between 4.0 and 4.6 g. Compared to their parental lines, the interspecific hybrids displayed variable responses under both irrigation levels.

3.2.8. Plant Dry Weight (PDW)

Plant dry weight followed a pattern similar to SDW (Table 2). Control plants of Tsakoniki accumulated more biomass (9.2 g), followed by ExSd (8.8 g) and LxSd (8.3 g), whereas *S. dasyphyllum* and *S. macrocarpon* had the lowest (5.5 and 5.6 g, respectively). It was evident that water stress was accompanied by substantial reductions in PDW in most genotypes, ranging between −29.2% and −38.4%. In contrast, *S. macrocarpon* and *S. dasyphyllum* again exhibited less sensitivity with non-significant low or moderate reductions. In

addition, no statistically significant differences among the genotypes were detected under stress conditions.



Figure 4. Representative roots of the studied genotypes under control (C) and water stress (WS) conditions. White box at bottom right indicates scale bar (10 cm). Genotype abbreviations: Emi, Langada, Tsakoniki (*S. melongena*, E, L, T), *S. dasyphyllum* (Sd), *S. macrocarpon* (Sm).

3.2.9. Root-to-Shoot Ratio

The highest root-to-shoot ratio under full irrigation was recorded in *S. dasyphyllum* (0.28) and *S. macrocarpon* (0.27), closely followed by the interspecific hybrids (0.25–0.27), indicating a more root-dominated growth pattern (Table 2). On the other hand, eggplant displayed a more shoot-oriented growth pattern with values ranging between 0.15 and 0.22. The changes in root-to-shoot ratio under water stress were not significant; however, two clear tendencies were identified. In *S. dasyphyllum*, TxSd and Langada, the ratio increased slightly to moderately, whereas in the remaining genotypes, it decreased to a similar extent. Under deficit irrigation, the highest values were recorded in *S. dasyphyllum* (0.33), TxSd (0.32) and *S. macrocarpon* (0.27), while eggplant cultivars maintained the lowest ratios (0.15–0.21).

3.3. Physiological Traits

3.3.1. Water Use Efficiency (WUE)

Water use efficiency differed significantly among genotypes under both irrigation treatments (Table 2). Under full irrigation, the highest WUE was recorded in the interspecific hybrids and the eggplant cultivars (2.5–3.0), which were clearly separated by *S. dasyphyllum* (1.6) and *S. macrocarpon* (1.9). Water stress imposed major increases in WUE in TxSd (26.0%), *S. dasyphyllum* (58.4%), and *S. macrocarpon* (62.4%), while the other genotypes displayed non-significant changes. The highest WUE under stress was observed in Tsakoniki, Langada,

the interspecific hybrids, and *S. macrocarpon* (3.0–3.3). In contrast, Emi and *S. dasyphyllum* recorded the lowest values (2.4 and 2.6, respectively).

3.3.2. Leaf Water Potential (LWP)

Leaf water potential was lower in the control plants of *S. dasyphyllum* (−12.8 bar) and its interspecific hybrids (−11.7 to −12.2 bar), whereas Tsakoniki (−7.3 bar) and *S. macrocarpon* (−8.8 bar) had the highest values. Water deficit significantly decreased LWP in most genotypes, with the exception of ExSd. The decrease was particularly pronounced in eggplant cultivars (−60.0 to −125.0%) and *S. macrocarpon* (−52.8%), while TxSd, LxSd, and *S. dasyphyllum* showed more moderate decreases (−17.7 to −24.3%). The lowest values of LWP under stress were observed in eggplant cultivars (ranging between −14.7 and −19.2 bar) and *S. dasyphyllum* (−15.0). The interspecific hybrids and *S. macrocarpon* showed the lowest values, ranging from −13.7 to −14.5 bar.

3.3.3. Relative Electrolyte Leakage (REL)

Electrolyte leakage showed no statistically significant differences between genotypes across treatments (Table 2). Under full irrigation, REL values ranged from 44.9% in Emi to 65.4% in ExSd. It was apparent that water stress generally increased REL, with significant increases recorded in Emi (71.2%), LxSd (56.4%) and TxSd (40.0%). The highest REL values in water-stressed plants were observed in LxSd (88.4%) and TxSd (83.6%), while the lowest were observed in Tsakoniki (59.2%) and *S. macrocarpon* (66.1%).

3.3.4. Chlorophyll Content Index (CCI)

Chlorophyll Content Index (CCI) was measured at 2, 3 and 4 weeks after the onset of water stress. CCI analysis revealed distinct patterns in chlorophyll retention across genotypes, irrigation levels and time (Table 2). At two weeks, CCI values in control plants ranged from 29.3 in Langada to 46.3 in *S. macrocarpon*. Water stress generally caused small or moderate increases in most genotypes; however, the only significant increase was recorded in TxSd (33.2%). The highest CCI under stress was again measured in *S. macrocarpon* (51.3) and TxSd (45.6), significantly higher than the other genotypes (32.1–40.9).

The highest CCI at three weeks under full irrigation was recorded in LxSd (67.8) and *S. macrocarpon* (64.3), while the lowest values were recorded in *S. dasyphyllum* (32.7), Emi (35.5), and Tsakoniki (36.7). Most genotypes showed only minor, non-significant changes in response to water stress. Notable exceptions were *S. macrocarpon*, with a moderate increase (28.5%), and ExSd and LxSd, which recorded moderate decreases (12.9% and 19.4%, respectively). *S. macrocarpon* exhibited the highest CCI (82.6) under deficit irrigation, clearly separated from the rest of the plant material, whereas *S. dasyphyllum* retained the lowest value (34.4).

At four weeks and under full irrigation, ExSd (64.8) and LxSd (64.0) exhibited the highest indices, while the lowest was recorded for Tsakoniki (33.9). Plants subjected to water stress showed non-significant increases or decreases, except for TxSd, where a significant increase in CCI by 24.4% was observed. Under stress, Tsakoniki (36.9), followed by *S. dasyphyllum* (41.3), had the lowest CCI compared to the rest of the plant material (49.3–63.2).

3.3.5. Malondialdehyde Content (MDA)

In the control treatment, the highest MDA content was recorded in LxSd and TxSd ($5.0 \mu\text{mol g}^{-1}$ fresh weight (FW)), while ExSd and *S. macrocarpon* displayed the lowest values ($3.7 \mu\text{mol g}^{-1}$ and $4.4 \mu\text{mol g}^{-1}$ FW, respectively). MDA levels under stress were not affected in ExSd, Langada, and *S. macrocarpon*, where only minor, non-significant changes occurred. In contrast, Emi displayed a sharp increase (90.0%), while Tsakoniki,

S. dasyphyllum, and LxSd showed significant reductions (−21.1%, −40.8%, and −31.7%, respectively). When grown under stress, Emi exhibited the highest value (7.8 $\mu\text{mol g}^{-1}$ FW), whereas *S. dasyphyllum* showed the lowest (2.5 $\mu\text{mol g}^{-1}$ FW).

3.4. Heterosis of the Interspecific Hybrids Under Control and Water Stress Conditions

Significant variation in both mid-parent (MPH) and better-parent heterosis (BPH) patterns was observed among the three interspecific hybrids (ExSd, LxSd, TxSd) under full and deficit irrigation conditions across all evaluated traits (Table 3, Figures 3 and 4).

Table 3. Mid-parent heterosis (MPH) and better-parent heterosis (BPH) in three *S. melongena* $\times$ *S. dasyphyllum* eggplant interspecific hybrids in control and water stress (WS) conditions.

Trait	Treatment	MPH			BPH		
		ExSd	LxSd	TxSd	ExSd	LxSd	TxSd
LL ¹	Control	5.11	1.13	−11.15 *	−1.31	−6.00	−21.88 *
	WS	−1.49	−7.76 *	−12.71 *	−4.96 *	−15.23 *	−16.57 *
LW	Control	0.43	−9.41	−22.22 *	−6.54	−12.37	−25.62 *
	WS	−9.77 *	−12.03	−29.8 *	−18.37 *	−21.48 *	−37.61 *
SD	Control	10.18 *	−4.15	1.23	−3.65	−19.11 *	−9.91 *
	WS	14.97 *	5.08	0.62	1.48	−8.59 *	−12.34 *
LN	Control	23.63 *	13.64 *	20.6 *	15.68 *	5.66	12.85 *
	WS	18.21 *	21.37 *	24.8 *	11.41	17.17 *	19.53 *
PH	Control	38.06 *	−9.42	3.26	−2.84	−40.05 *	−28.73 *
	WS	20.61 *	3.02	4.0	−15.84 *	−30.20 *	−27.22 *
LAI	Control	62.3 *	57.26 *	42.42 *	51.15 *	52.07 *	24.50 *
	WS	81.46 *	32.86 *	62.42 *	59.30 *	8.14 *	55.81 *
RDW	Control	51.52 *	55.36 *	10.32	48.31 *	47.46 *	−4.91
	WS	28.05 *	28.49	4.35	−1.87	7.48	0.93
SDW	Control	42.77 *	17.29 *	3.72	26.30 *	−4.91	−18.48 *
	WS	26.6 *	19.9	−7.44	14.85	2.83	−20.91
R/S	Control	6.38	28.57 *	2.04	−7.41	0.00	−7.41
	WS	−8.33	−2.04	18.52 *	−33.33 *	−27.27 *	−3.03
PDW	Control	44.43 *	23.63 *	4.99	31.10 *	4.26	−16.07 *
	WS	26.64 *	21.69	−5.0	23.21 *	10.71	−15.78
WUE	Control	43.35 *	40.71 *	9.48	18.78 *	13.26 *	−16.17 *
	WS	33.47 *	9.35	9.4	30.59 *	−0.64	−3.03
LWP	Control	11.04	1.48	14.54	−4.55	−8.47 *	−9.80
	WS	−6.77	−15.13 *	−13.21	−7.80	−24.36 *	−17.15 *
REL (%)	Control	24.58 *	−3.11	5.62	8.85	−5.94	−0.63
	WS	−8.23	24.93 *	26.47 *	−10.56	21.10	14.52
CCI 2 w	Control	8.32	−8.07	−11.15	−2.58	−17.47	−14.86
	WS	11.12	−8.63	21.69 *	7.86	−11.16	11.59
CCI 3w	Control	55.6 *	66.58 *	28.99 *	49.49 *	39.31 *	22.02 *
	WS	36.29 *	39.63 *	41.73 *	34.51 *	24.25 *	35.75 *
CCI 4w	Control	23.41 *	33.32 *	13.18	13.95	32.93 *	−3.49
	WS	17.14	39.46	47.81 *	2.16	28.13 *	39.91 *
MDA	Control	−9.49	20.58 *	23.25 *	−10.14	20.14 *	21.01 *
	WS	−26.47 *	4.59 *	25.71 *	−51.61 *	−16.38 *	11.75

¹ LL, leaf length (cm); LW, leaf width (cm); SD, stem diameter (mm); LN, leaf number; PH, plant height (cm); LAI, leaf area index; RDW, root dry weight (g); SDW, shoot dry weight (g); R/S, root-to-shoot ratio; PDW, plant dry weight (g); WUE, water use efficiency (g L^{-1}); LWP, leaf water potential; REL, relative electrolyte leakage; CCI 2 w, CCI 3 w, CCI 4 w, chlorophyll content index at 2, 3 and 4 weeks; MDA, malondialdehyde content ($\mu\text{mol g}^{-1}$). ns and * indicate, respectively, non-significant and significant differences ($p < 0.05$) between the hybrid and the respective mid-parent value for MPH and better-parent value for BPH.

Under full irrigation, several traits expressed significant positive or negative MPH. For example, TxSd exhibited negative heterosis for leaf length (−11.5%). For leaf number, all hybrids were heterotic, with MPH values ranging from 13.6% in LxSd to 23.6% in ExSd, while ExSd also showed marked increases in plant height (38.1%) and leaf area index (62.3%). The other hybrids also showed considerable MPH for these traits. Both ExSd and LxSd exhibited substantial positive heterosis for root dry weight (51.5% and 55.4%, respectively), shoot dry weight (42.8% and 17.3%, respectively), and pod dry weight (44.4% and 23.6%, respectively), as well as for water use efficiency (43.4% and 40.7%, respectively). Chlorophyll content indices were particularly enhanced, especially at three and four weeks, where all hybrids recorded large gains (55.6 to 66.6%). In contrast, negative MPH was evident in TxSd for leaf length (−11.2%) and leaf width (−22.2%), while MDA showed opposing trends, with increases in LxSd (20.6%) and TxSd (23.3%) but reductions in ExSd (−26.5%).

In addition, BPH was observed in ExSd, which outperformed the better parent in several traits, including leaf number (15.7%), leaf area index (51.2%), root dry weight

(48.3%), shoot dry weight (26.3%), plant dry weight (31.1%), water efficiency (18.8%), and CCI at three weeks (49.5%). LxSd and TxSd also demonstrated BPH in CCI (39.3% and 22.0%, respectively), but both showed reduced plant height compared to the superior parent (−40.1% and −28.7%). Negative BPH was also apparent in leaf traits, e.g., in TxSd for leaf length (−21.9%) and leaf width (−25.6%) and in ExSd for MDA (−51.6%), indicating that hybrid vigor was not uniformly expressed across all traits. Overall, under full irrigation, ExSd was the most heterotic hybrid.

Under water stress, MPH was evident in several traits, though its expression varied among hybrids (Table 3, Figures 3 and 4). All hybrids retained MPH for leaf number, which ranged from 18.2% in ExSd to 24.8% in TxSd, while ExSd again showed the highest MPH in leaf area index (81.5%). ExSd was superior for biomass allocation, displaying positive MPH for root, shoot and plant dry weight (28.1%, 26.6% and 26.6%, respectively). Chlorophyll content was again strongly enhanced, particularly at three weeks, ranging from 36.3% in ExSd to 41.7% in TxSd. TxSd also maintained the highest values even at four weeks (47.8%). Interestingly, MDA again showed a contrasting pattern, with ExSd recording a reduction (−26.5%), while LxSd (4.6%) and TxSd (25.7%) exhibited increases, suggesting different stress response strategies.

At the better-parent level, ExSd maintained its superior performance under stress, showing positive heterosis for leaf area index (59.3%), plant dry weight (23.2%), water use efficiency (30.6%), and CCI at three weeks (34.5%). LxSd and TxSd also displayed advantages in leaf number (17.2% and 19.5%, respectively) and CCI at four weeks (28.1% and 39.9%). However, negative BPH was observed in all hybrids for plant height (−27.2 to −30.2%), leaf length (−5.0 to 16.6%) and leaf width (−18.4 to 37.6%). MDA once again distinguished the hybrids: ExSd recorded negative BPH (−16.4%), while LxSd and TxSd showed positive values (20.1% and 11.8%, respectively), consistent with their higher oxidative stress markers.

3.5. Correlation Analysis

3.5.1. Correlations Under Full Irrigation Conditions

Significant correlations were observed among various agronomic and physiological traits in the control group (Figure 5a). Leaf length (LL) showed moderate positive correlations with leaf width (LW), stem diameter (SD), and shoot dry weight (SDW). SD exhibited strong correlations with plant height (PH), SDW, and water use efficiency (WUE). PH was positively correlated with multiple traits, including leaf number (LN), SDW, and plant dry weight (PDW). As expected, PDW was highly correlated with SDW, as well as with root dry weight (RDW). Considering the physiological traits, WUE was strongly associated with biomass-related traits, including SDW and PDW. Interestingly, the root-to-shoot ratio (R/S) was negatively correlated with plant height and stem diameter but positively correlated with RDW. The chlorophyll content index at 2 weeks (CCI 2 w) was negatively correlated with PH and LN but positively with relative electrolyte leakage (REL). Later CCI measurements (at 3 weeks and 4 weeks) were positively associated with LAI and RDW.

3.5.2. Correlations Under Deficit Irrigation Conditions

Water stress shifted the correlation patterns, as fewer significant associations were detected (Figure 5a,b). LL maintained a moderate positive correlation with LW and PH, whereas LW exhibited moderate to strong negative correlations with both LN and PH. SD was moderately to strongly positively correlated with SDW, PDW, and WUE, while it showed strong negative correlations with R/S and PH. RDW was moderately and negatively correlated with PH and MDA but strongly and positively associated with R/S. PDW and SDW were strongly interrelated, and both traits were strongly and positively

associated with WUE. CCI at 2 weeks showed moderate positive correlations with RDW and WUE. Later CCI measurements (at 3 weeks and 4 weeks) were sequentially and positively associated. CCI at 3 weeks showed a moderate negative correlation with PH. MDA exhibited moderate positive correlations with PH and CCI at 4 weeks, while it was moderately to strongly negatively correlated with RDW and R/S.

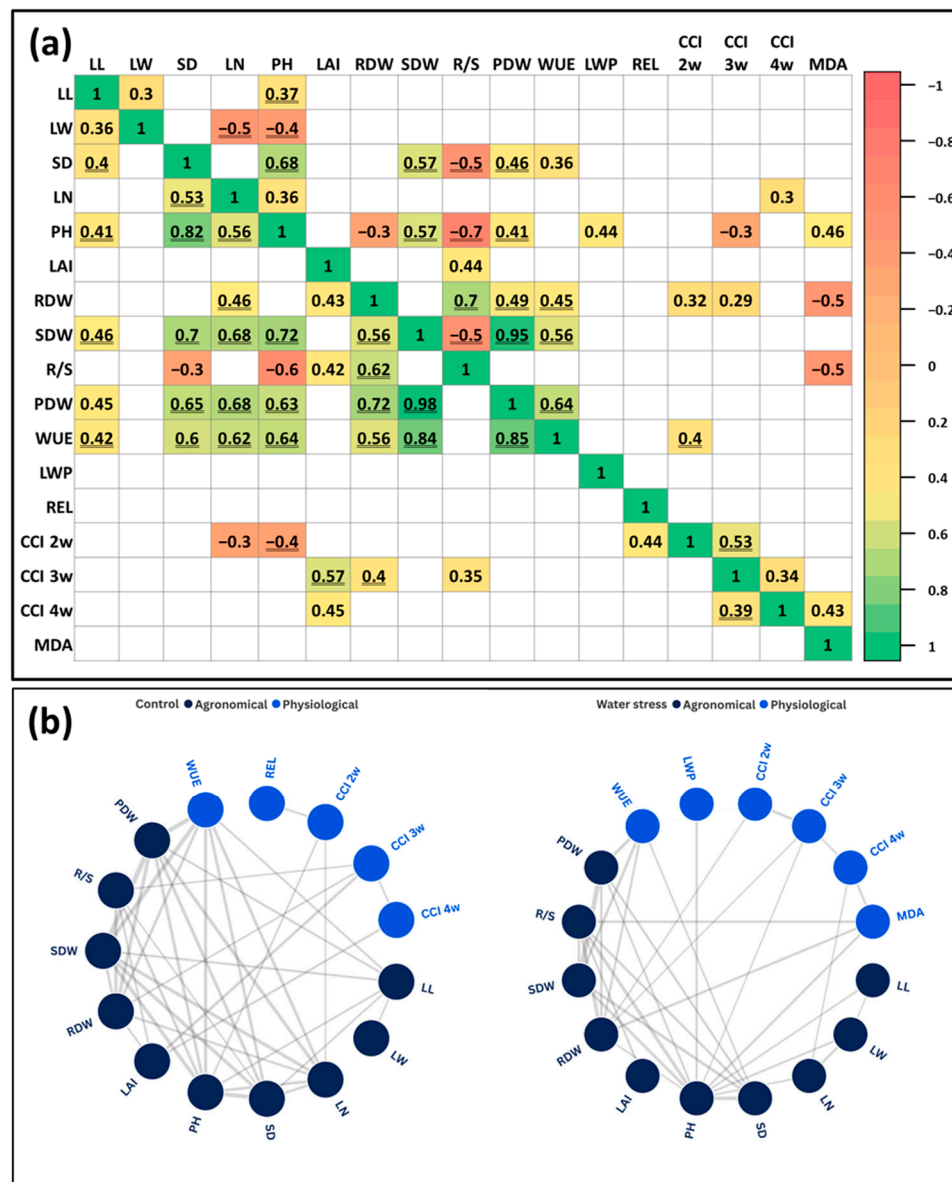


Figure 5. (a) Correlation coefficient matrix of agronomic and physiological traits under control (upper diagonal) and water stress (lower diagonal) conditions across eight genotypes. Only significant correlations at $p < 0.05$ are shown, while those significant at $p < 0.01$ are underlined. (b) Correlation networks under control (left) and water stress (right) conditions.

3.6. Principal Component Analysis (PCA)

The first two principal components (PC1 and PC2) of the PCA accounted for 57.2% of the observed variation, with PC1 and PC2 explaining 37.2% and 20.0% of the variation, respectively (Figure 6). It was observed that all agronomic traits, with the exception of R/S, were positioned on the positive side of the PC1 axis. In contrast, most physiological traits, except for MDA, were located on the negative side. The chlorophyll content indices were grouped together with R/S in the upper left quadrant, while WUE, LWP, and REL were positioned in the lower left quadrant of the loading plot. PC1 showed high positive

correlations (>0.5) with SDW, PDW, PH, LL, LN, SD, RDW, and LAI, and high negative correlations (<-0.5) with LWP and REL. PC2 displayed strong positive correlations with R/S, LAI, and RDW, and strong negative correlations with PH and SD. Correlations of a lesser magnitude were observed for LW, CCI 2 w, CCI 3 w, and WUE across the two factors, whereas MDA and CCI 4w showed weaker associations with both PC1 and PC2.

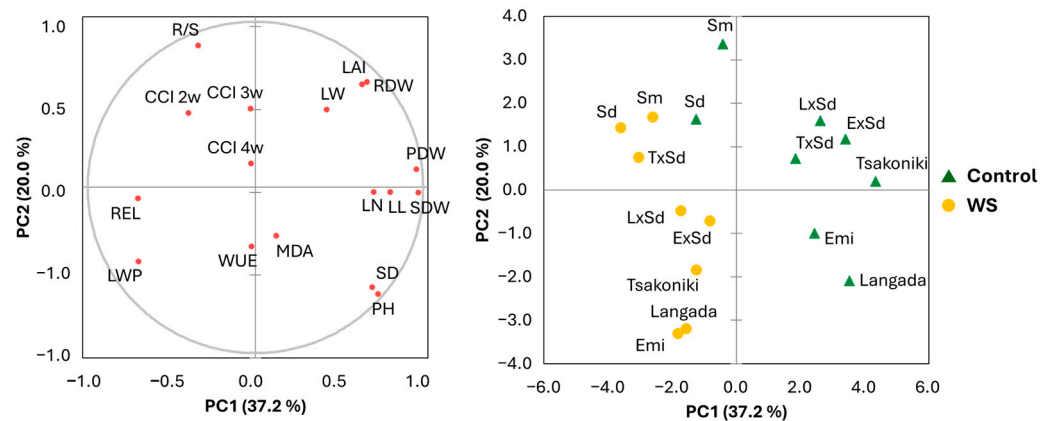


Figure 6. Loading plot of traits (left) and score plot of genotypes and treatments (right) from the principal component analysis of agronomic and physiological traits across eight genotypes under control and water stress conditions. The plots were based on the first and second principal components (PC1 and PC2), explaining 37.2% and 20.0% of variation, respectively.

In the score plot, a clear separation of genotypes according to treatment was evident along the PC1 axis, with control treatments generally located on the right side and water stress treatments on the left. An exception was observed for *S. macrocarpon* and *S. dasyphyllum*, which displayed similar positions under both irrigation regimes. Control treatments of the interspecific hybrids were grouped in the upper right quadrant, while the eggplant cultivars Emi and Langada were positioned in the lower right quadrant, with Tsakoniki located near the PC1 axis but closer to the hybrids. Under water stress, the eggplant cultivars clustered in the lower left quadrant together with LxSd and ExSd, the latter positioned closer to the PC1 axis. Both treatments of *S. macrocarpon* and *S. dasyphyllum*, together with TxSd, were located in the upper left quadrant.

4. Discussion

Sensitivity to drought has been previously reported in eggplant, tomato, pepper, and other cultivated *Solanum* species, which are known to exhibit limited tolerance to water deficit due to their physiological and genetic makeup [21]. That was also confirmed in the present study, as water stress strongly affected the growth and physiology of the plant material. This sensitivity may be attributed to the evolutionary history of these crops [2]. Furthermore, the loss of genetic variation through domestication and intensive breeding has likely reduced the diversity of alleles associated with stress tolerance.

Genotype-specific responses to drought have been previously reported in eggplant and various *Solanum* species, including wild and cultivated species [26,53,54]. Our findings also revealed contrasting drought responses among the plant material studied, evidenced by the significant genotypic effect on agronomic and physiological parameters, as well as actual and relative performance under water stress. In practice, our results support that considerable genetic variability exists in the eggplant gene pool for the improvement of the crop's drought tolerance.

4.1. Genotypic Responses to Water Stress

In general, under full irrigation, the eggplant cultivars outperformed *S. dasyphyllum* and *S. macrocarpon* but proved very sensitive to water stress, as evidenced by the greater reductions observed in the agronomic traits studied. The general good stability of *S. dasyphyllum* under drought conditions possibly reflects adaptability traits linked to its origin in semi-arid habitats. *S. macrocarpon*, despite being a domesticated form of *S. dasyphyllum*, showed remarkable tolerance to drought stress, surpassing, for certain traits, its ancestor. It is possible that *S. macrocarpon* inherited some of the drought tolerance traits from *S. dasyphyllum* and/or acquired new traits through domestication.

A typical adaptive strategy in plants facing drought stress is to limit the transpiration surface and minimize water loss [55]. Previous studies have demonstrated that severe drought stress in eggplant leads to significant reductions in both leaf size and leaf number [14,56]. In the present study, reduction in leaf dimensions, leaf number, and consequently, leaf area index was a common water stress response in most genotypes (Table 2). Eggplant and the interspecific hybrids displayed reductions in both leaf dimensions, particularly in width, as well as in leaf number, with the hybrids appearing somewhat less sensitive than their cultivated parents. In *S. macrocarpon*, drought stress caused a pronounced reduction in LAI but only a slight decrease in leaf number, while *S. dasyphyllum*, which exhibited the smallest overall reduction in LAI, showed only modest decreases in both leaf size and leaf number. These contrasting patterns suggest that different mechanisms are employed by different species to limit transpiration surface under drought conditions.

Drought generally reduces stem thickness and plant height in eggplant and related *Solanum* species [14,23,57–59]. In the present study, deficit irrigation reduced height in all genotypes; however, the reductions recorded in *S. macrocarpon* and *S. dasyphyllum* were minimal, especially in the former, which was practically unaffected (Table 2). This may be related to more efficient biomass allocation and retention of growth under water stress, indicative of drought tolerance. The interspecific hybrids were somewhat less affected than their respective eggplant parents, suggesting partial inheritance of drought tolerance from *S. dasyphyllum*. There was a tendency for stem diameter to decrease under stress; however, only eggplant Langada exhibited a significant decrease, possibly reflecting a higher sensitivity.

Biomass accumulation in eggplant can be severely affected by drought, and retention of biomass can serve as a tolerance index [9,23]. Our results confirmed this type of sensitivity. Under full irrigation, the cultivated eggplant genotypes accumulated higher biomass than *S. dasyphyllum* and *S. macrocarpon*, probably due to the slower growth rate of the African species. However, under water stress, *S. macrocarpon* practically maintained its biomass, indicating superior drought tolerance than eggplant and most interspecific hybrids, while *S. dasyphyllum* showed an intermediate response, with moderate reductions under water stress.

A common drought adaptation in plants is the increased biomass allocation to roots, improving soil exploration and water uptake. Genotypes with higher root-to-shoot ratios are generally more tolerant to drought [60,61]. In our study, *S. dasyphyllum* and *S. macrocarpon*, despite producing less total biomass, showed higher root dry weight and root-to-shoot ratios than the eggplant cultivars Emi and Langada (Table 2). This shared trait of *S. dasyphyllum* and *S. macrocarpon* may reflect adaptation to similar environmental pressures. Only Tsakoniki had a greater root dry weight, but with a lower root-to-shoot ratio and a greater reduction under stress compared to the African species. It is not uncommon for local cultivars, such as Tsakoniki, to exhibit drought tolerance traits, including enhanced root development [23]. Interestingly, the interspecific hybrids combined higher root biomass

than both parents, with higher root-to-shoot ratios than their eggplant parents, suggesting potential value as rootstocks for eggplant grafting.

Our results highlight a clear genotypic variation in physiological responses to water stress, consistent with previous studies that reported significant diversity among cultivated, wild or hybrid relatives of eggplant in drought tolerance mechanisms [6,44,59,62]. The higher water use efficiency (WUE) observed in interspecific hybrids and in some cultivars under full irrigation indicates an improved ability to convert available water into biomass or productivity (Table 2). In contrast, the lower WUE in *S. dasyphyllum* and *S. macrocarpon* under full irrigation likely reflects different survival strategies, such as drought escape through reduced growth [56]. On the other hand, WUE increased substantially under water stress, most notably in *S. dasyphyllum*, *S. macrocarpon*, and TxSd, suggesting optimized mechanisms to avoid reduced transpiration via stomatal closure and/or osmotic adjustment that maintain photosynthesis and biomass accumulation despite reduced water availability.

Leaf water potential decreased in all genotypes under drought, reflecting reduced water availability in plant tissues. Cultivated varieties maintained the lowest values under stress, showing greater sensitivity to water stress, while the interspecific hybrids and *S. macrocarpon* exhibited higher values. Interestingly, *S. macrocarpon*, despite being the less drought-sensitive genotype, experienced a great decrease in leaf water potential (−52.8%). This implies that other mechanisms than osmotic regulation are involved in drought tolerance. On the other hand, *S. dasyphyllum*, which also showed a good drought tolerance, had one of the lowest values of leaf water potential under full irrigation and exhibited stability under stress, indicating a different mechanism than *S. macrocarpon*.

Electrolyte leakage is an indicator of membrane stability under abiotic stress [63]. In the present study, water stress induced clear increases in REL in certain genotypes, particularly Emi, LxSd, and TxSd, suggesting a higher susceptibility of cellular membranes to drought-induced damage. In contrast, *S. macrocarpon*, ExSd and Tsakoniki were not affected under stress, indicating more effective membrane protection mechanisms, possibly linked to enhanced antioxidant activity as stress tolerance adaptation in *Solanum* species [64]. The contrasting responses observed here are indicative of the genotype-dependent responses.

While severe water stress can reduce chlorophyll content, moderate stress may lead to its increase [8,58,59]. During the experimental period, *S. macrocarpon* and the hybrid TxSd maintained the highest CCI, whereas *S. dasyphyllum* and the cultivar Tsakoniki consistently exhibited the lowest values (Table 2). These results suggest that *S. macrocarpon* and selected genotypes are more efficient in preserving photosynthetic pigments under deficit irrigation. Nevertheless, the relatively low CCI of *S. dasyphyllum* did not impair its performance, as it ranked second in drought tolerance after *S. macrocarpon*. Similar increases in photosynthetic pigments under stress have been reported in other *Solanum* species, such as *S. aethiopicum* hybrids exposed to salinity [65]. Interestingly, in the latter case, chlorophyll levels initially increased and later stabilized, showing an analogy with the overall trend observed in our study.

In this study, contrasting responses among eggplant cultivars, wild and cultivated relatives, and interspecific hybrids were observed for malondialdehyde (MDA) content under water stress. While Emi exhibited a sharp increase, indicative of enhanced oxidative damage, Tsakoniki, *S. dasyphyllum*, and LxSd showed significant reductions, and other genotypes, such as ExSd, Langada and *S. macrocarpon*, exhibited a degree of stability in oxidative stress markers under water stress. Similar stability for MDA levels has been reported in wild eggplant relatives [27]. In contrast, Tani et al. [54] reported a consistent increase in MDA and H₂O₂ across two evaluated genotypes under reduced irrigation, pointing to strong oxidative stress induction. Such discrepancies may reflect differences in genetic backgrounds, stress duration, and experimental conditions. These findings

suggest that oxidative stress responses to drought in eggplant and related species are highly genotype-dependent, and potential tolerance mechanisms exist in stable materials.

The contribution of different traits in the observed variation is reflected in the PCA variable scatterplot (Figure 6). The first component (PC1) was mainly associated with growth and biomass-related traits (shoot and plant dry weight, plant height, leaf number, and leaf length), indicating that this axis represents overall plant vigor and productivity. In contrast, the second component (PC2) was mainly influenced by root and physiological traits such as chlorophyll indices and leaf water potential. This separation suggests that while PC1 reflects the overall growth performance of the genotypes, PC2 captures adaptive strategies of the plant. In addition, the PCA score plot allowed for the separation of genotypes across treatment groups, divided by the vertical axis (PC2). Interestingly, under water stress, the different genotypic groups were positioned more closely together (Figure 6). Such discrimination has been reported in similar eggplant studies on cultivated and wild eggplant genotypes [6,59,62].

4.2. *S. macrocarpon* and *S. dasyphyllum* Have Different Drought Avoidance Adaptations

S. macrocarpon and *S. dasyphyllum* were more drought resilient than *S. melongena* and the interspecific hybrids studied, as demonstrated by the relative agronomic and physiological performance under full and deficit irrigation (Table 2, Figures 3 and 4). However, their contrasting responses to deficit irrigation revealed alternative adaptive strategies, which can be attributed to their different evolutionary histories. *S. dasyphyllum* exhibited more pronounced reductions in plant biomass and stem diameter under stress, while simultaneously increasing its root-to-shoot ratio and retaining more leaf area. This pattern suggests an adaptive response centered on biomass reallocation, favoring root development. By contrast, *S. macrocarpon*, which has been subjected to domestication, maintained plant biomass, plant height, and leaf number under deficit irrigation, showing only minimal reductions in growth and a considerable reduction in leaf area. These observations suggest an efficient water retention strategy associated with reduced transpiration surface. In addition, *S. macrocarpon* has been reported as a desiccation-tolerant species [25], maintaining PSII efficiency and limiting ROS accumulation under severe dehydration, which may relate to the retained chlorophyll content and minimal biomass reduction observed in our study.

Other possible mechanisms worth investigating in the future include leaf traits, as *S. macrocarpon* leaves are rigid, glabrous, and macroscopically lack trichomes, with previous studies reporting a very low density of glandular hair [66] and a distinct cuticular wax profile compared to other *Solanum* species [67]. On the other hand, *S. dasyphyllum* leaves have trichomes, which may contribute to drought avoidance by reducing transpiration. Trichome density has been associated with enhanced water use efficiency and lower transpiration rates in *Solanum* species and tomatoes [68].

Together, these results demonstrate that two closely related species have adopted distinct pathways to cope with water limitation. Such complementary strategies highlight their value as genetic resources for eggplant improvement, offering opportunities to combine different drought-adaptive traits in breeding programs.

4.3. Heterosis Was Retained Under Different Irrigation Conditions

The results showed that heterosis of the interspecific hybrids was expressed in several key traits under both irrigation regimes, with ExSd consistently outperforming the parental lines for biomass allocation, leaf area index, chlorophyll content, and water use efficiency (Table 3, Figures 3 and 4). This type of stress resilience could be inherited by *S. dasyphyllum* or arise from the hybrid nature of the genotype. In popcorn maize, heterosis under drought

stress has been reported to be governed by non-additive genes [69]. Similarly, overdominant and underdominant gene action contributed to maize heterosis under drought stress [70].

While the magnitude of heterosis was reduced in water stress, it was still significant for traits like leaf number, biomass accumulation and water use efficiency, indicating the buffering capacity of certain interspecific hybrids against drought. Retainment of heterosis in drought conditions has also been reported in maize [69,70], soybean [71] and faba bean [72]. TxSd and LxSd showed less consistent performance than ExSd; however, they still exhibited positive heterosis for specific traits under deficit irrigation. This suggests a varying degree of stress tolerance depending either on the effect of each eggplant cultivar's genome per se or in combination with the genome of *S. dasyphyllum* or even reciprocal parental effects as reported by Kamphorst et al. [69].

From another point of view, the heterotic effects observed for agronomic traits support the potential use of these interspecific hybrids as rootstocks. Grafting onto vigorous or stress-tolerant rootstocks is a well-established strategy to improve drought resilience, nutrient uptake, and overall plant vigor [73]. In eggplant grafting on interspecific hybrids and wild relatives is a common practice contributing to enhanced growth, yield and disease resistance [40–43]. In this context, ExSd appears particularly promising, as it combines high heterosis with relative stability under stress, making it a valuable genetic resource for rootstock breeding.

4.4. Water Stress Shifted Correlation Networks

The comparative correlation analysis between full and deficit irrigation revealed distinct trait interrelationships, possibly reflecting adaptation strategies (Figure 5). Under full irrigation, significant positive correlations among agronomic traits, particularly vegetative growth (stem diameter, plant height, leaf number) and biomass traits (shoot, plant, and root dry weight and water use efficiency), indicate the coordination in vegetative growth development in the absence of stress.

However, under water stress, the correlation structure shifted, reducing the magnitude of growth trait correlations, emphasizing root-related traits and reducing the overall number of significant correlations. Such widening of correlation patterns under stress has been reported in eggplant and introgression eggplant lines [6,62]. In the present study, root dry weight was negatively correlated with plant height, reflecting a potential investment toward root rather than shoot development. The negative association of leaf width with leaf number and plant height may suggest a trade-off between leaf expansion and water conservation by minimizing transpiration surface, a common adaptation in plants [46].

In addition, significant correlations between some physiological and growth traits emerged. For example, root dry weight, leaf number and WUE were positively correlated with chlorophyll content, perhaps due to a sustained photosynthetic capacity and efficient distribution of assimilates. In addition, the negative correlations of the oxidative marker MDA with root dry weight and root-to-shoot ratio probably reflect the ability of plants with strong root biomass allocation to mitigate oxidative stress. Similar patterns have been reported in various eggplant materials subjected to water stress [6,62].

4.5. Implications for Eggplant Breeding

S. macrocarpon, *S. dasyphyllum*, and selected hybrids exhibited promising drought resilience based on agronomic and physiological data, and their performance highlights their potential for improving drought tolerance in eggplant. Notably, the fact that drought tolerance was achieved through different mechanisms suggests that crosses between *S. macrocarpon* and *S. dasyphyllum* could produce hybrid genotypes with even greater levels of drought tolerance, potentially combining complementary drought-adaptive traits [2].

While *S. dasyphyllum* performed worse than *S. macrocarpon*, it is still a valuable breeding resource because it readily produces fertile hybrids with *S. melongena*, facilitating the transfer of adaptive traits through conventional breeding approaches such as interspecific crosses, backcrossing, and conventional or marker-assisted selection [32,38].

In contrast, *S. macrocarpon*, despite exhibiting better drought resilience in our experiments, has limited crossability with eggplant and produces sterile interspecific hybrids [29]. Sterile hybrids often require genome duplication to restore fertility and subsequently anther culture to return to the diploid state or the production of double haploid plants [74], making the breeding process complex and resource-intensive. Therefore, a different strategy is needed to incorporate useful alleles from *S. macrocarpon* into eggplant.

Finally, the hybrid vigor exhibited by the interspecific hybrids in this study indicates a potentially valuable germplasm for rootstock breeding. For more efficient and economical production of the interspecific rootstocks, available eggplant CMS lines could be used as female parents in the crosses [42,75].

While this study provides valuable information on plant responses to water stress, the experimental setup using potted seedlings may not fully reflect field conditions and plant responses during the reproductive stage, which are crucial for fruit production and quality. Future studies should validate these results under open-field or greenhouse growing environments and across different developmental stages.

4.6. Policy Implications and Future Prospects

The identification of drought-resilient genotypes provides valuable information for breeding programs aiming to improve climate resilience in eggplant cultivation. These findings support the potential of developing cultivars and rootstocks and better adaptation to lower inputs and water scarcity by using cultivated or wild (crop wild relatives; CWR) germplasm. From a policy perspective, promoting the protection and utilization of CWR resources could contribute to sustainable agriculture, particularly in regions facing increasing water limitations due to climate change. Future research should focus on field validation of promising genotypes, multi-location trials, and integration of molecular tools to accelerate breeding efforts.

5. Conclusions

This study demonstrates the contrasting drought responses of cultivated eggplant, its African relatives *S. dasyphyllum* and *S. macrocarpon*, and their interspecific hybrids. Cultivated eggplant proved highly sensitive to water stress, whereas the African species showed complementary tolerance mechanisms: *S. dasyphyllum* through root allocation and leaf maintenance, and *S. macrocarpon* via structural and biochemical adaptations. Hybrid heterosis was retained to a considerable degree in stress conditions, enhancing biomass and root traits, thus offering potential as drought-tolerant rootstocks. Trait correlations under stress indicated trade-offs between growth and water conservation, highlighting the role of roots and physiological stability for homeostasis under drought. These results support the use of wild relatives and interspecific hybrids in breeding drought-resilient eggplant genotypes, with field validation and targeted breeding approaches as essential next steps.

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Appendix A

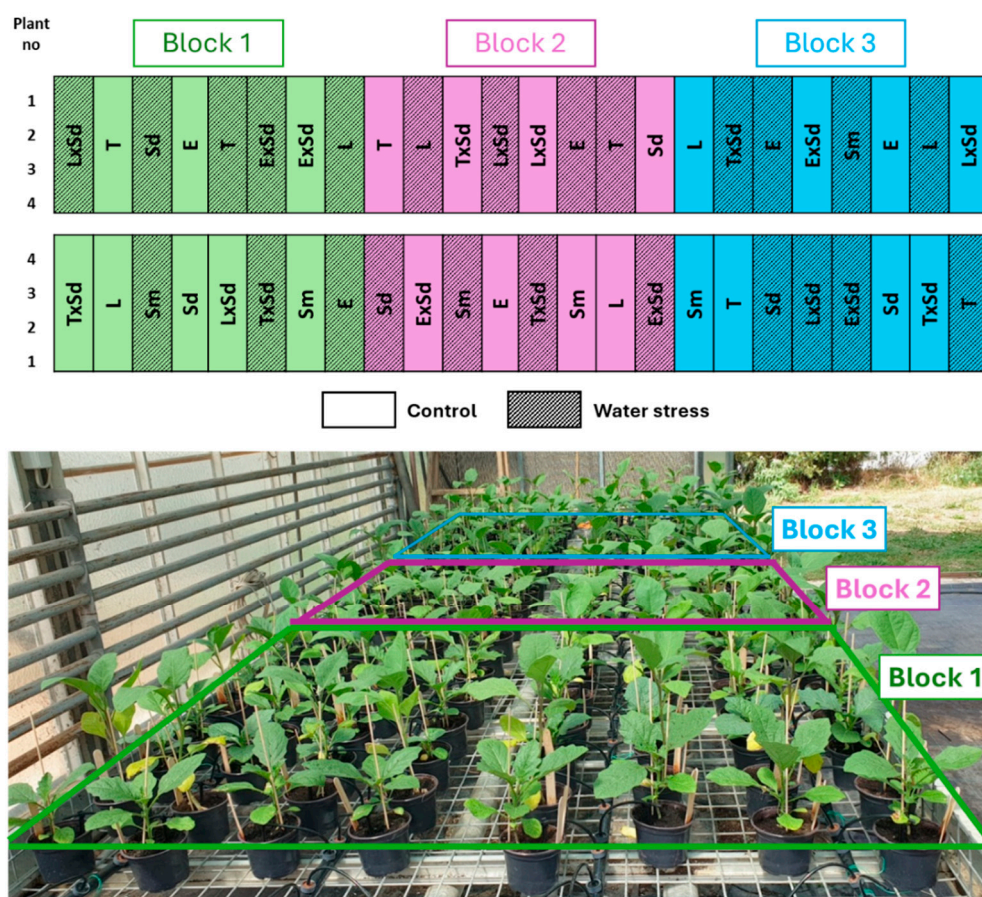


Figure A1. Experimental RCBD layout (**above**) and representative view of the greenhouse experiment (**below**). Abbreviations: *Solanum melongena* Emi, Langada and Tsakoniki (E, L and T, respectively), *S. dasyphyllum* (Sd) and *S. macrocarpon* (Sm).

Table A1. ANOVA table obtained from the statistical analysis of agronomical and physiological traits.

Trait	Statistic	Source of Variation					
		Genotype	Irrigation Level	Genotype × Irrigation Level	Block	Error	Total
LL ¹	Sum of Squares	105.367	96.436	25.512	5.497	171.760	404.572
	Df	7	1	7	2	126	143
	Mean Square	15.052	96.436	3.645	2.749	1.363	
	F	11.042	70.744	2.674	2.016		
	Sig.	0.000	0.000	0.013	0.137		
LW	Sum of Squares	66.248	54.025	7.282	6.102	241.900	375.557
	Df	7	1	7	2	126	143
	Mean Square	9.464	54.025	1.040	3.051	1.920	
	F	4.930	28.140	0.542	1.589		
	Sig.	0.000	0.000	0.801	0.208		
SD	Sum of Squares	38.811	4.161	5.773	1.050	48.180	97.975
	Df	7	1	7	2	126	143
	Mean Square	5.544	4.161	0.825	0.525	0.382	
	F	14.500	10.882	2.157	1.373		
	Sig.	0.000	0.001	0.042	0.257		
LN	Sum of Squares	81.624	34.132	4.790	1.417	65.210	187.173
	Df	7	1	7	2	126	143
	Mean Square	11.661	34.132	0.684	0.709	0.518	
	F	22.531	65.950	1.322	1.369		
	Sig.	0.000	0.000	0.245	0.258		

Table A1. Cont.

Trait	Statistic	Source of Variation					
		Genotype	Irrigation Level	Genotype × Irrigation Level	Block	Error	Total
PH	Sum of Squares	2072.389	359.764	129.609	3.228	590.700	3155.690
	Df	7	1	7	2	126	143
	Mean Square	296.056	359.764	18.516	1.614	4.688	
	F	63.151	76.740	3.949	0.344		
	Sig.	0.000	0.000	0.001	0.709		
LAI	Sum of Squares	7.568	11.031	1.153	0.009	1.840	21.602
	Df	7	1	7	2	30	47
	Mean Square	1.081	11.031	0.165	0.005	0.061	
	F	17.628	179.856	2.687	0.075		
	Sig.	0.000	0.000	0.028	0.928		
RDW	Sum of Squares	2.974	3.271	0.752	0.416	9.980	17.393
	Df	7	1	7	2	126	143
	Mean Square	0.425	3.271	0.107	0.208	0.079	
	F	5.363	41.298	1.357	2.624		
	Sig.	0.000	0.000	0.229	0.077		
SDW	Sum of Squares	37.793	49.591	10.903	1.660	77.369	177.317
	Df	7	1	7	2	126	143
	Mean Square	5.399	49.591	1.558	0.830	0.614	
	F	8.793	80.762	2.537	1.351		
	Sig.	0.000	0.000	0.018	0.263		
R/S	Sum of Squares	0.150	0.000	0.025	0.008	0.000	0.182
	Df	7	1	7	2	126	143
	Mean Square	0.021	0.000	0.004	0.004	0.002	
	F	9.326	0.005	1.557	1.672		
	Sig.	0.000	0.944	0.154	0.192		
PDW	Sum of Squares	47.915	77.029	16.024	3.218	116.848	261.034
	Df	7	1	7	2	126	143
	Mean Square	6.845	77.029	2.289	1.609	0.927	
	F	7.381	83.063	2.468	1.735		
	Sig.	0.000	0.000	0.021	0.181		
WUE	Sum of Squares	8.556	4.279	2.483	0.702	13.576	29.596
	Df	7	1	7	2	126	143
	Mean Square	1.222	4.279	0.355	0.351	0.108	
	F	11.344	39.715	3.292	3.257		
	Sig.	0.000	0.000	0.003	0.042		
LWP	Sum of Squares	63.692	254.206	102.379	16.977	321.839	759.094
	Df	7	1	7	2	126	143
	Mean Square	9.099	254.206	14.626	8.489	2.554	
	F	3.562	99.522	5.726	3.323		
	Sig.	0.002	0.000	0.000	0.039		
REL	Sum of Squares	998.511	3129.379	1666.648	287.118	12,904.992	18,986.648
	Df	7	1	7	2	126	143
	Mean Square	142.644	3129.379	238.093	143.559	102.421	
	F	1.393	30.554	2.325	1.402		
	Sig.	0.214	0.000	0.029	0.250		
CCI 2 w	Sum of Squares	1975.019	190.004	278.484	508.714	4781.287	7733.508
	Df	7	1	7	2	126	143
	Mean Square	282.146	190.004	39.783	254.357	37.947	
	F	7.435	5.007	1.048	6.703		
	Sig.	0.000	0.027	0.401	0.002		
CCI 3 w	Sum of Squares	9265.481	0.230	1336.596	238.336	7293.472	18,134.115
	Df	7	1	7	2	126	143
	Mean Square	1323.640	0.230	190.942	119.168	57.885	
	F	22.867	0.004	3.299	2.059		
	Sig.	0.000	0.950	0.003	0.132		
CCI 4 w	Sum of Squares	4615.424	1.876	618.025	273.606	10,940.877	16,449.808
	Df	7	1	7	2	126	143
	Mean Square	659.346	1.876	88.289	136.803	86.832	
	F	7.593	0.022	1.017	1.575		
	Sig.	0.000	0.883	0.423	0.211		
MDA	Sum of Squares	5.945	0.360	6.592	0.012	10.787	23.696
	Df	7	1	7	2	126	143
	Mean Square	0.849	0.360	0.942	0.006	0.086	
	F	9.921	4.205	10.999	0.072		
	Sig.	0.000	0.042	0.000	0.931		

¹ LL, leaf length (cm); LW, leaf width (cm); SD, stem diameter (mm); LN, leaf number; PH, plant height (cm); LAI, leaf area index; RDW, root dry weight (g); SDW, shoot dry weight (g); R/S, root-to-shoot ratio; PDW, plant dry weight (g); WUE, water use efficiency (g L⁻¹); LWP, leaf water potential; REL, relative electrolyte leakage; CCI 2 w, CCI 3 w, CCI 4 w, chlorophyll content index at 2, 3 and 4 weeks; MDA, malondialdehyde content (μmol g⁻¹).

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