

Article

Detection of Epistasis for Seed and Some Phytochemical Traits in Coriander under Different Irrigation Regimes

Mehrdad Hanifei ¹, Shaghayegh Mehravi ², Mostafa Khodadadi ³, Anita Alice Severn-Ellis ² , David Edwards ²  and Jacqueline Batley ^{2,*} 

¹ Department of Plant Genetics and Breeding, Faculty of Agriculture, Tarbiat Modares University, Tehran 14115-336, Iran; mehanifei@gmail.com

² School of Biological Sciences, University of Western Australia, Perth, WA 6009, Australia; Shaghayegh.mehravi@uwa.edu.au (S.M.); anita.severn-ellis@uwa.edu.au (A.A.S.-E.); dave.edwards@uwa.edu.au (D.E.)

³ Seed and Plant Improvement Institute, Agricultural Research Education and Extension Organization (AREEO), Karaj 33151-31359, Iran; mkhodadadi@spii.ir

* Correspondence: jacqueline.batley@uwa.edu.au; Tel.: +61-8-64885929

Abstract: Coriander (*Coriander sativum* L.) is an annual herb mainly cultivated for its seed characteristics. Drought stress is a major problem which affects coriander behaviour through biochemical responses. This study aimed to determine the nature and magnitude of epistasis in inheritance of seed yield (SY), percent of dehulled seed (PODS), percent of seed hulls (POSH), essential oil content (EOC), essential oil yield (EOY), dehulled seed fatty acid content (DSFAC), hull fatty acid content (HFAC), fatty acid content (FAC), and fatty acid yield (FAY), and to estimate additive and dominance variance for the traits not influenced by epistatic effects. Three testers, TN-59-158 (highly drought-susceptible), TN-58-230 (highly drought-tolerant, but low-yielding), and their F₁ hybrid were each crossed for six genotypes. The experiment was performed under different levels of water deficit: control (C), moderate water deficit (MWD), and severe water deficit (SWD) conditions. Epistasis affected the expression of SY, EOC, EOY, FAC, and FAY in all water conditions, PODS in C, POSH in SWD, HFAC in MWD, and DSFAC in both C and MWD conditions. Total epistatic effects were partitioned, showing that both [i] and [j + l] type interactions were significant, with a prevalent influence of [i] type interactions on these traits except for POSH and FAC in the SWD condition, which exhibited a higher value of the [j + l] type. Both additive and non-additive gene actions were significant for those traits not significantly affected by epistasis in C, MWD, or SWD conditions. An additive type of gene action was preponderant for PODS in MWD and SWD, POSH in MWD, DSFAC in SWD, and HFAC in C and SWD conditions.

Keywords: *Corianderum sativum* L.; drought stress; modified triple test cross; epistasis; gene action



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1. Introduction

The cost of petroleum-derived products has increased during the last decade, and considering the rapid reduction in world fossil fuel resources there is a clear need to identify alternative sources [1]. Among a broad variety of sources considered, agricultural products are potential sources of industrial raw materials. Sustainable industrial crops have thus emerged as a new source of strategic industrial raw materials. While strategies for improving the fatty acid profile and composition of oils generated by existing crops are being explored, another strategy is to look for alternative species as possible sources of specialized oils. An example of such a crop is coriander (*Coriander sativum* L.). Its oils contain a high concentration of fatty acids and essential oils [2]. The composition, stability, and extraction methods of fatty acid and essential oil are different [1]. Hydrodistillation is used to extract essential oils, whereas extraction or pressing is used to obtain fatty oils. In the case of fatty acids, seeds contain 9–21% fatty acid, of which petroselinic (C18:1n-12),

oleic (C18:1n-9), and linoleic (C18:2n-6) acids are the main components. Petroselinic acid can be oxidatively cleaved to lauric (C12:0) and adipic (C6) acids. Lauric acid is a compound useful in the production of emulsifiers, detergents, soaps, and softeners, and adipic acid can be utilized in the synthesis of a variety of polymers, including Nylon 6,6. Furthermore, fatty acid methyl esters are excellent fuels due to their superior low-temperature properties, high oxidative stability, and lower iodine content [3]. Evangelista et al. [4] reported different oil contents in coriander seed parts. The oil content of whole coriander seeds (17.6%) was less than that of dehulled seed oil (37.6%), showing that hulls attract a remarkable amount of oil.

Coriander seeds contain 0.3–1.2% essential oils, of which 60–70% is linalool. This is widely used as a flavoring in the food industry. Despite the importance of essential oils for numerous industrial purposes, their production in quantities exceeding 1 t y^{-1} is restricted to fewer than 60 cultivated plants from 21 species in the Apiaceae family, which includes coriander [5]. Among these 60 crops, coriander had the maximum annual seed production amount and value in 2016 [6].

Drought is a worldwide problem that seriously influences the production of agricultural crops [6–8]. There are several reports that conditions with limited water can significantly change fatty acid and essential oil yield in cumin [9,10], soybean [11], sage [12], caraway [13], purple basil [14], and coriander [8]. Water deficit stress can have positive impacts on secondary metabolite production [15].

Knowledge of the extent and nature of the genetic systems control and heritability of the quantitative traits is essential for any applied breeding program [16]. Some studies on the analysis of genetics for seed, fatty acid, and essential oil yield in coriander are available, but these are invariably based on models of second-degree statistics developed assuming the absence of epistasis or non-allelic interactions. Epistasis plays a key role in the inheritance of economic traits in several crops [17–24]. In the presence of epistasis, estimates of additive and dominance components of genetic variation are biased to an unknown extent [25,26]. This may affect a breeding program by causing an inappropriate breeding method to be chosen [27]. The most reliable method currently available for accurate detection of the presence of epistasis is the triple test cross (TTC), which is a modification of the “North Carolina III” design and can be used regardless of the allele frequencies, gene correlations, degree of inbreeding, and mating system of the populations to be investigated [28]. Later, Jinks et al. [29] proposed a modification known as a modified triple test cross (MTTC), in which the testers L_1 and L_2 were crossed with several genotypes instead of random F_2 individuals as suggested by Kearsey and Jinks [30].

In this study, the detection of epistatic, additive, and dominance components of coriander seed yield or its seed quality characters under different watering conditions using the MTTC was performed. The knowledge of the genetic control mechanism of seed yield and its seed quality characters under different irrigation regimes will be useful for selection of the most efficient breeding method to develop promising coriander genotypes.

2. Materials and Methods

2.1. Plant Material

The plant material used in this study was selected based on a preliminary experiment to screen endemic Iranian coriander genotypes under drought stress [6]. Two genotypes, viz. TN-59-158 (origin: Hamadan) and TN-59-230 (origin: Bushehr), were utilized as testers with L_1 and L_2 designation, respectively. They were 2 extremes for drought tolerance and seed yield. TN-59-158 is highly drought-susceptible but high-yielding, whilst TN-59-230 is highly drought-tolerant but very low-yielding. Furthermore, the TN-59-158 \times TN-59-230 hybrid was used as third tester, designated as L_3 . Phenotypic differences between the testers and male parents are shown in Figure 1. To construct MTTC generations, all crosses between 6 genotypes of TN-59-353 (G_1 , relatively drought-tolerant, origin: Markazi), TN-59-80 (G_2 , drought-susceptible, origin: Isfahan), commercial (G_3 , origin: Alborz), TN-59-347 (G_4 , drought-tolerant, origin: Lorestan), TN-59-160 (G_5 , drought-tolerant and relatively

high-yielding, origin: Mazandaran), and TN-59-10 (G_6 , drought-tolerant, origin: Yazd) as male parents and L_1 , L_2 , and L_3 as female parents took place from January to November 2015. Thus, the MTTC generations consisted of 9 parents (3 testers and 6 males), 12 single crosses, and 6 three-way crosses.

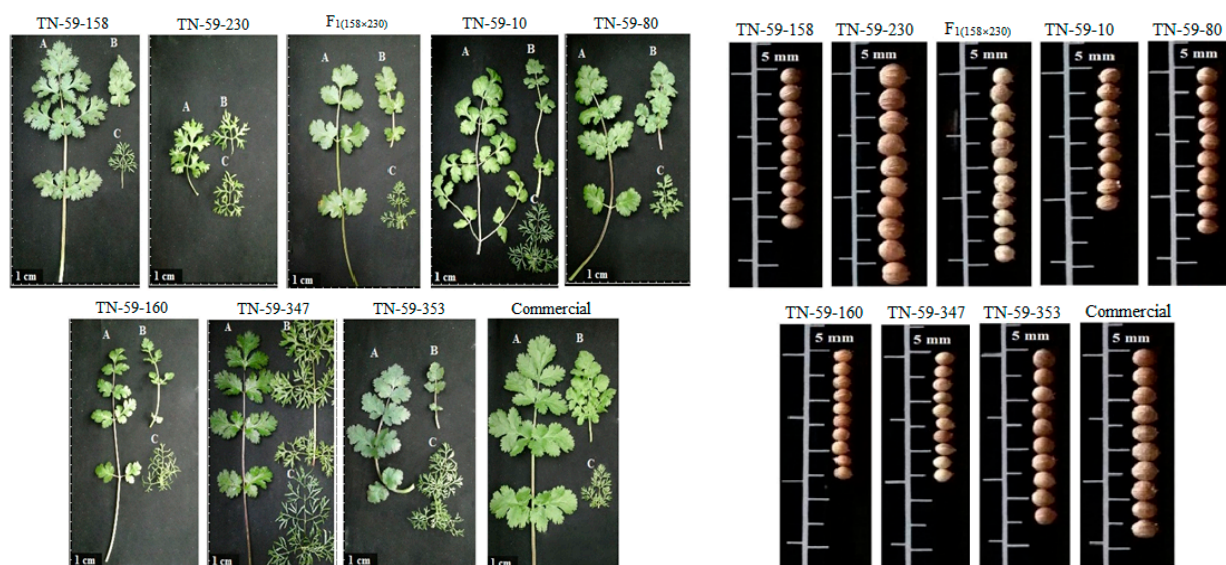


Figure 1. Seed, leaf form, and size of testers and genotypes used in the modified triple test cross. (A) longest basal, (B) middle, and (C) top leaves, respectively.

2.2. Experimental Site and Growth Conditions

The experiment was implemented at the research field of Tarbiat Modares University in Tehran, Iran ($51^{\circ}09' E$; $35^{\circ}44' N$, at an altitude of 1265 m above sea level). Before sowing, the seeds were disinfected in sodium hypochlorite solution (10%) (Sigma-Aldrich, Saint Louis, MI, USA) for 5 min and then fixed in ethanol (96%) for 1 min and rinsed in distilled water thereafter [31]. The 9 parents, 12 single crosses, and 6 three-way crosses were evaluated with different levels of water deficit (C, MWD, SWD) with a randomized complete block design with 3 replications. In the C regime, genotypes were kept well-watered. For MWD, genotypes were well-irrigated until the commencement of stem elongation, when watering was withdrawn until the end of the flowering stage. Then, recovery water was applied once. In the SWD experiment, watering was like that of C until the commencement of the flowering stage, after which watering was cut off completely [32]. The field's soil had a sandy loam structure consisting of 15% silt, 15% clay, and 70% sand with 700 and 125 mg kg^{-1} K and P, respectively, as well as 0.12% N, 1.21% organic carbon and 21.1% fixed carbon. The soil had a relatively low electrical conductivity of 1.01 dS m^{-1} . The field daily vapor pressure deficit (VPD), corresponding precipitation, and rainy days are presented in Figure 2.

The mean relative humidity and mean temperature values were 19% and 23.5°C at 7:00 a.m., 12% and 35.5°C at 2:00 p.m., and 20% and 26.0°C at 9:00 p.m., respectively. A plot size of 2 m^2 (a 2-row plot of 2 metres in length) was assigned to each entry, consisting of 14 plants in each replication. The plant-to-plant spacing between and within rows was kept at 30 cm and 40 cm, respectively, in the 3 experiments. The watering dates and frequencies are shown in Figure 3 for each of the populations.

2.3. Seed Yield Measurement

The seed yield of testers and male parents were measured using 10 plants and 20 plants for entries obtained from single and 3-way crosses, respectively. The percentages of dehulled seeds (PODS) and of seeds hulls (POSH) were measured to investigate the effect of water deficit stress.

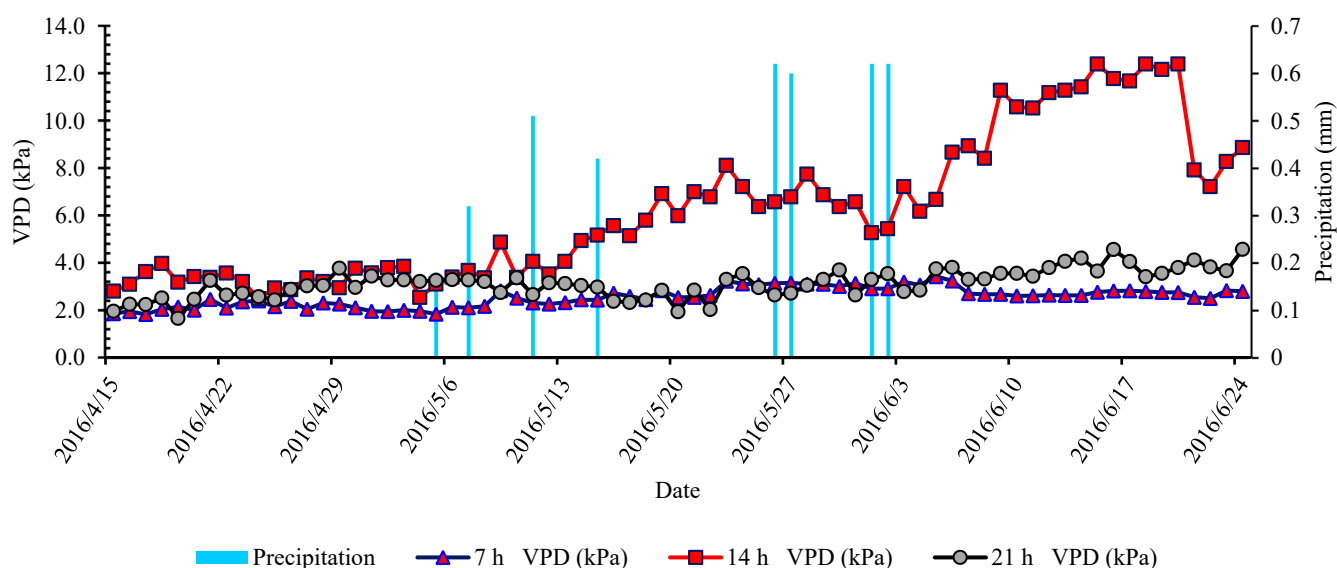


Figure 2. Average daily (24 h) vapor-pressure deficit (VPD) value and number of rainy days after commencement of the tests. VPD and precipitation (mm) in the field tests at 7:00 a.m., 2:00 p.m., and 9:00 p.m., and rainy days.

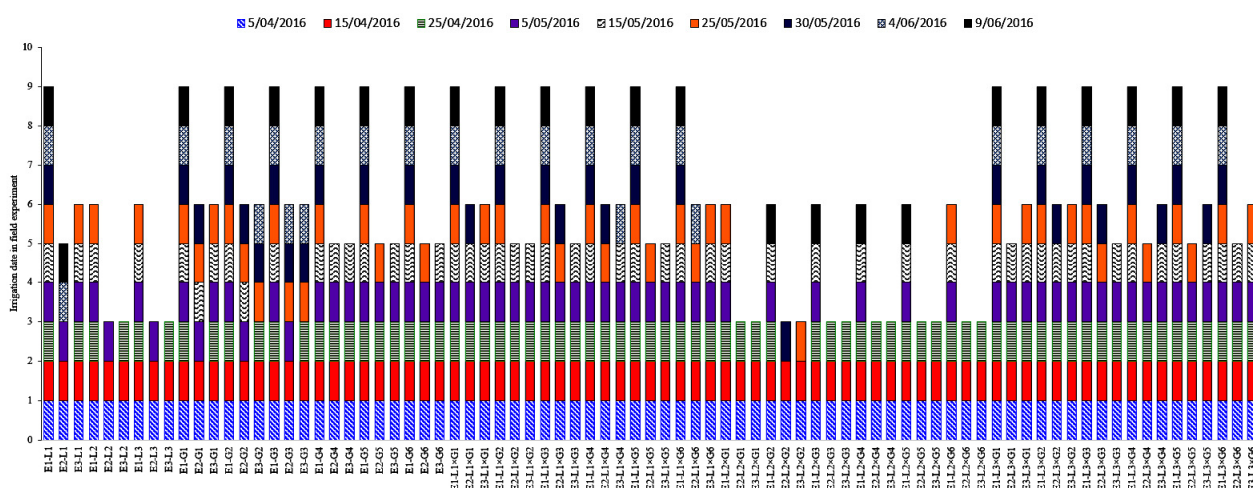


Figure 3. Irrigation times of genotypes in field experiments, e.g., E₁L₁, E₂L₁, and E₃L₁ show the irrigation period of tester 1 under control (C), moderate water deficit (MWD), and severe water deficit (SWD) conditions, respectively.

2.4. Essential Oil Extraction

The essential oil content (EOC) of seeds was extracted using a Clevenger-type apparatus. Air-dried seeds were triturated in an electric grinder. In total, 30 grams of triturated seed samples were subjected to 250 mL water distillation for 2 h using a Clevenger-type apparatus. The EOC (%w/w) was measured as the weight (g) of EO per 100 g of seed [32]. Furthermore, EOY was computed as the weight (g) per plant seed sample. To evaluate the effect of water deficit stress on EOC, the primary EOC was adjusted by PODS values.

2.5. Fatty Acid Extraction

Fatty acid contents from coriander seeds and dehulled seeds with different hull contents were extracted using a Soxhlet extractor. The dehulling of seeds was done using a soft edge blade electric grinder and then the hulls were separated by an air fan. Hulls and dehulled seeds were triturated in an electric grinder. Then, approximately 2 g of each triturated material were extracted in a Soxhlet extractor with 250 mL of petroleum ether for 6 h. The extract was then filtered, with evaporation of the solvent under reduced

pressure and temperature [10]. The FAC (%w/w) was determined as the weight (g) of oil per 100 g of hull/seeds. Furthermore, FAY was calculated as the weight (g) per plant.

2.6. Statistical Analysis

2.6.1. Analysis of Variance

Analysis of variance was performed using the model suggested by Singh and Chaudhary [33] to determine the significance of treatments and to partition the treatment effect to determine the significance of variation among hybrids, parents, genotypes, testers, $P_1 + P_2$ vs. F_1 , P_1 vs. P_2 , genotypes vs. testers, and hybrids vs. parents for each of the traits using the MTTC technique. Excel (Excel, 2013) and SAS (SAS 9.1, 2003) software were used for data analysis and graphs, respectively.

2.6.2. Test for Epistasis

The detection of epistasis was performed according to Singh and Chaudhary [33]. The test of significance of the $L_{1j} + L_{2j} - 2L_{3j}$ (j = genotype) provides information about the presence or absence of epistasis. Therefore, for each genotype and each replication the $L_{1j} + L_{2j} - 2L_{3j}$ was calculated and then tested. The total epistasis for 6 degrees of freedom was calculated on the total replications according to Equation (1).

$$\text{Total sum of square of epistasis} = \left[\sum \frac{(L_{1j} + L_{2j} - 2L_{3j})^2}{n} \right] \quad (1)$$

The total epistatic effect was divided into the [i] type (homozygote \times homozygote) with 1 degree of freedom and the [j + l] type of epistasis (heterozygote \times heterozygote and homozygote \times heterozygote) with 5 degrees of freedom. The sums of squares of [i] and [j + l] were calculated according to Equations (2) and (3).

$$\text{Sum of square i type} = \frac{[\sum (L_{1j} + L_{2j} - 2L_{3j})]^2}{n} \quad (2)$$

$$\text{Sum of square [j + l]} = \left[\sum \frac{(L_{1j} + L_{2j} - 2L_{3j})^2}{n} \right] - \frac{[\sum (L_{1j} + L_{2j} - 2L_{3j})]^2}{n} \quad (3)$$

The sum of squares due to interaction of epistasis with blocks was calculated as the difference between the total sum of squares of epistasis and the sum of squares for the type of epistasis in question (total, [i] type or [j + l] type). Each of the 3 types of epistasis was tested against its respective interaction with blocks. However, before testing individual epistasis effects, the homogeneity of the interaction was firstly tested. Homogeneity of [i] \times block and [j + l] \times block interaction variances was tested using an “F” test with 2 and 10 degrees of freedom according to Equation (4).

$$F(2, 10) = \frac{\text{Mean square of i type inteaction}}{\text{Mean square of j and l type inteaction}} \quad (4)$$

2.6.3. Individual Genotypic Epistasis

The individual contribution of each genotype to total epistasis was determined and tested for significance from 0 for those traits in which the total epistasis was significant. The mean value $\sum (L_{1j} + L_{2j} - 2L_{3j}) / r$ of each genotype for a trait was tested using a “t” test with 12 degrees of freedom according to Equation (5).

$$t = \frac{\text{Mean}}{\sqrt{\frac{\text{Error mean square}}{r}}} \quad (5)$$

2.6.4. Additive Dominance Model

For those traits in which epistasis was not detected an additive dominance was fitted to the data [29,30].

Estimation of the Additive (D) and Dominance (H) Variance Components of Variation

For estimation of the additive and dominance components, the sum ($L_{1i} + L_{2i}$) and difference ($L_{1i} - L_{2i}$) for each genotype was calculated replication-wise and subjected to an analysis of variance (Table 1) [33].

Table 1. Analysis of variance for estimation of the additive and dominance components.

Source of Variation	df	Sum		Difference	
		MS	Expected MS	MS	Expected MS
Replications	$r - 1$	MS_r		MS_r	
Sums ($L_{1i} + L_{2i}$)	$n - 1$	MS_s	$\sigma_e^2 + 2r\sigma_s^2$		
Difference ($L_{1i} - L_{2i}$)	$n - 1$			MS_d	$\sigma_e^2 + 2r\sigma_d^2$
Error	$(r - 1)(n - 1)$	MS_e	σ_e^2	MS_e	σ_e^2

Where r = number of replications; n = the number of genotypes; MS_r , MS_s , MS_d , and MS_e = mean squares of replications, sums, differences, and error, respectively; and σ_e^2 , σ_s^2 , and σ_d^2 = variance components due to error, sums, and differences, respectively.

Finally, the values of D and H were calculated using Equations (6) and (7), respectively.

$$D = 8(MS_s - MS_e)/2r \quad (6)$$

$$H = 8(MS_d - MS_e)/2r \quad (7)$$

Average Degree of Dominance

The average degree of dominance was calculated as $(H/D)^{1/2}$, where H and D are the dominance and additive variance components, respectively.

Direction of Dominance

The linear correlation coefficient between the sums and corresponding differences ($r_{s,D}$) for all genotypes was determined as direction of dominance.

Broad-Sense Heritability and Narrow-Sense Heritability

Broad-sense heritability (h_B^2) and narrow-sense heritability (h_N^2) were calculated according to Equations (8) and (9) [23].

$$h_B^2 = \frac{\frac{1}{2D} + \frac{1}{4H}}{V_P} \quad (8)$$

$$h_N^2 = \frac{\frac{1}{2D}}{V_P} \quad (9)$$

3. Results

3.1. Irrigation Regime Influence on Measured Traits

WT had a significant effect on all traits ($p < 0.01$). Furthermore, there was a significant interaction between genotype and water treatment for all measured traits. The mean values of SY, EOY, and FAY decreased 46%, 53%, and 50% in MWD conditions, and 54%, 50%, and 50% in SWD conditions. The reduction of some genotypes in MWD conditions was greater than with SWD and vice versa for other genotypes (Figure 4). As for SY, EOY, and FAY, EOC and FAC decreased by 10% and 14%, respectively, in MWD conditions. Furthermore, the seed hull-to-dehulled seed mass ratio significantly increased under water

deficit stress (Figure 5). The PODS of genotypes were differently affected in MWD and SWD conditions. The FAY reduced due to water deficit stress in all genotypes except in L_2 and $H_{L_2 \times G_6}$, which had more FAY in SWD conditions. In general, the $H_{L_3 \times G_4}$ hybrid exposed the greatest mean value for SY and FAY in C conditions. $H_{L_2 \times G_2}$ and $H_{L_3 \times G_4}$ hybrids had the greatest mean value of FAY and SY in MWD conditions. Furthermore, in SWD conditions the $H_{L_2 \times G_2}$ and $H_{L_2 \times G_5}$ had the greatest mean value of SY and FAY, respectively (Figure 4). As shown in Figure 5, the reduction in PODS was greater than that of the POSH, which led to an increase in the hull-to-dehulled seed mass ratio.

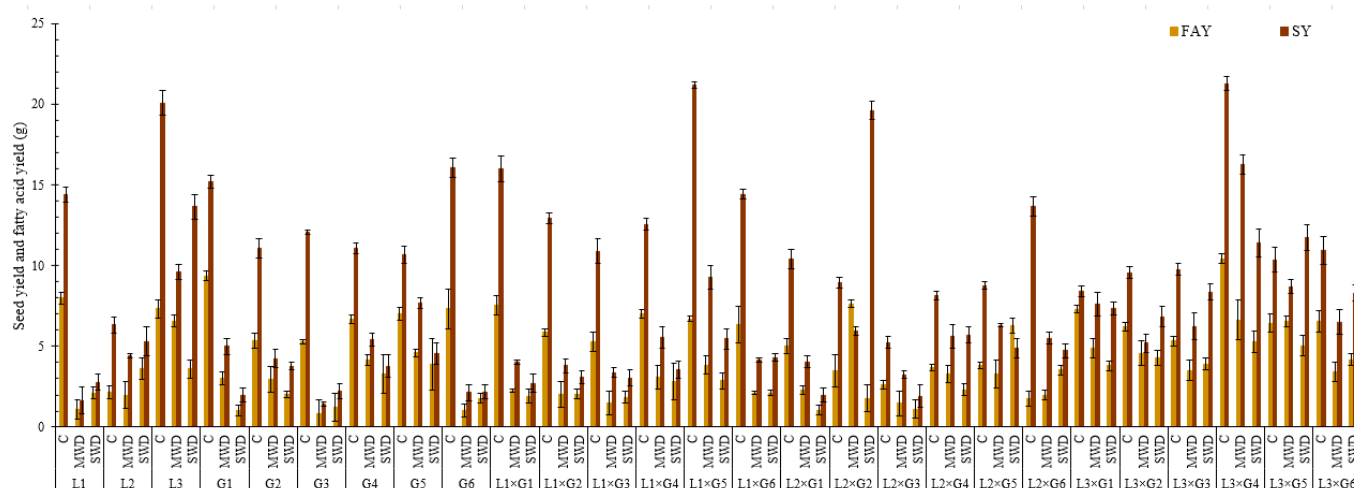


Figure 4. Water treatment (WT) \times genotype interaction effect on seed yield (SY) and fatty acid yield (FAY). C: control; MWD: moderate water deficit; SWD: severe water deficit. L_1 – L_3 : three testers, G_1 – G_6 : 6 male parents; L_1G_1 – L_2G_6 : 12 single hybrids; and L_3G_1 – L_3G_6 : 6 three-way hybrids in a modified triple test cross.

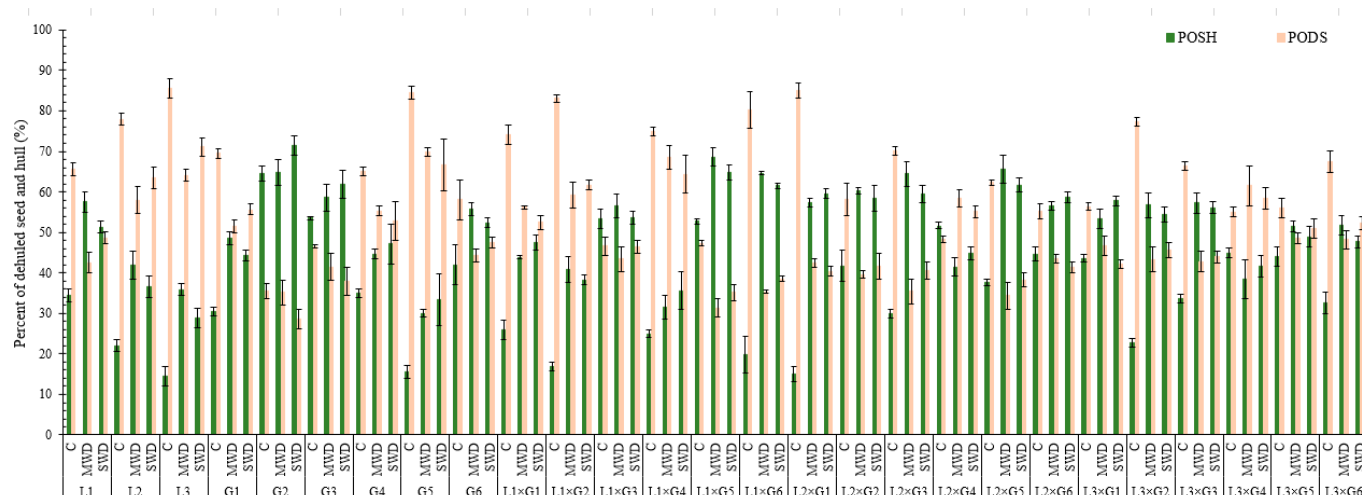


Figure 5. Water treatment (WT) \times genotype interaction effect on the percent of seed hulls (POSH) and percent of dehulled seed (PODS). C: control; MWD: moderate water deficit; SWD: severe water deficit. L_1 – L_3 : 3 testers, G_1 – G_6 : 6 male parents; L_1G_1 – L_2G_6 : 12 single hybrids; and L_3G_1 – L_3G_6 : 6 three-way hybrids in a modified triple test cross.

The genotypes showed different responses to irrigation regimes for HFAC, DSFAC, and FAC (Figure 6). In C, MWD, and SWD conditions, the greatest mean value of FAC was detected for the $H_{L_2 \times G_5}$, $H_{L_2 \times G_6}$, and L_2 , respectively. The EOC, adjusted essential oil content (AdjEOC), and EOY exhibited significant water treatment \times genotype interactions (Figure 7). Furthermore, $H_{L_3 \times G_5}$ in C, L_3 and $H_{L_2 \times G_2}$ in C and MWD, and $H_{L_3 \times G_5}$ in SWD conditions exhibited the greatest mean values of EOC, EOY, and AdjEOC, respectively.

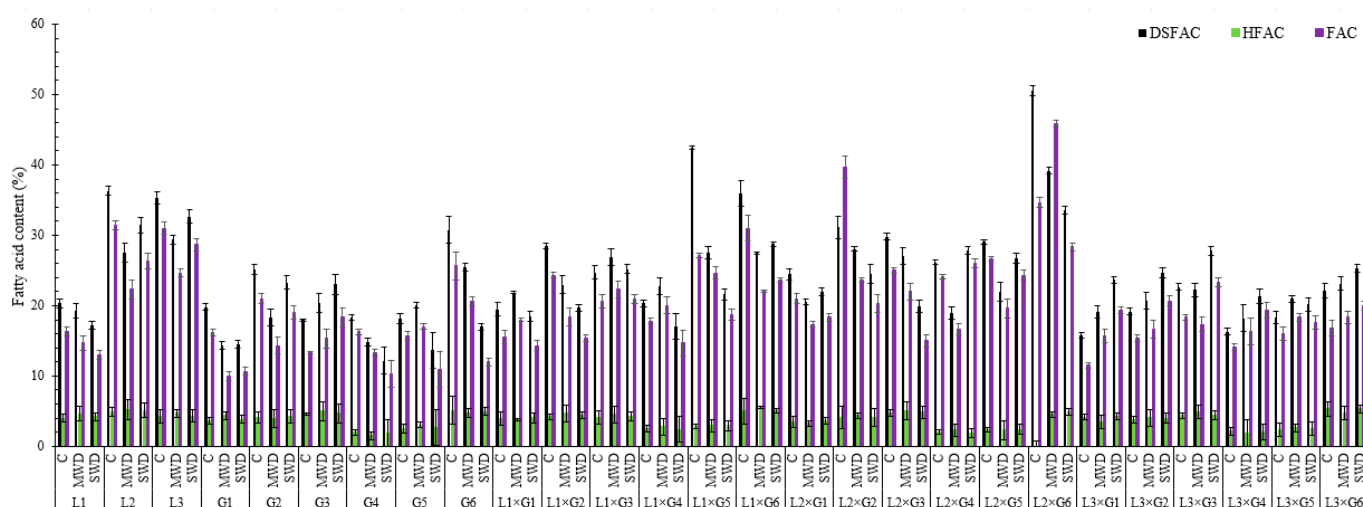


Figure 6. Water treatment (WT) \times genotype interaction effect on dehulled seed fatty acid content (DSFAC), hull fatty acid content (HFAC), and whole fatty acid content (FAC). C: control; MWD: moderate water deficit; SWD: severe water deficit. L₁–L₃: 3 testers, G₁–G₆: 6 male parents; L₁G₁–L₂G₆: 12 single hybrids, and L₃G₁–L₃G₆: 6 three-way hybrids in a modified triple test cross.

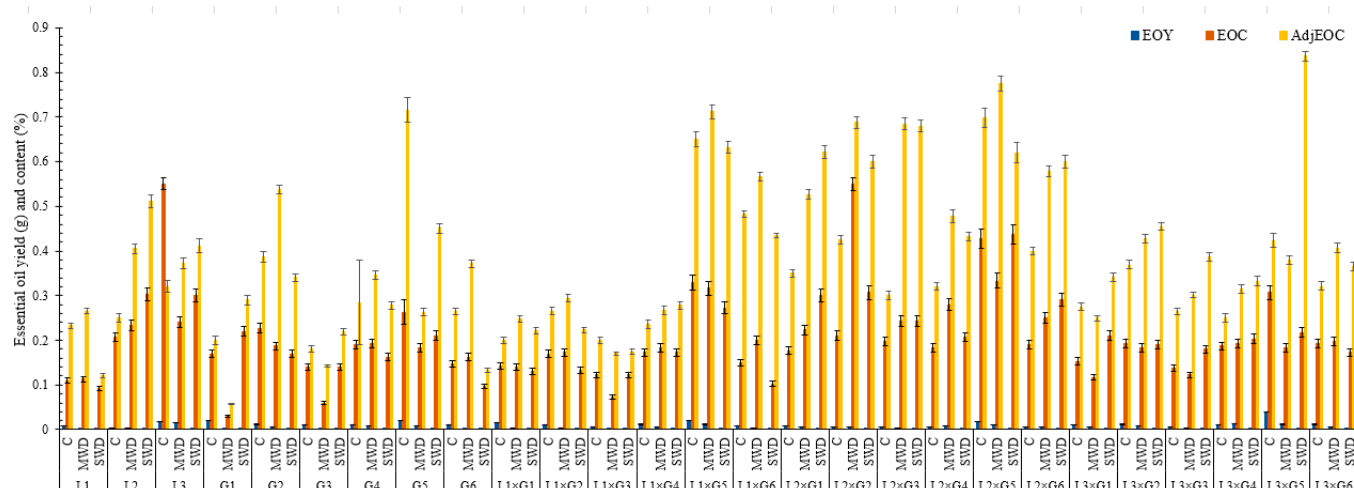


Figure 7. Water treatment (WT) \times genotype interaction effect on essential oil content (EOC), essential oil yield (EOY), and L₁–L₃: 3 testers, G₁–G₆: 6 male parents; L₁G₁–L₂G₆: 12 single hybrids, and L₃G₁–L₃G₆: 6 three-way hybrids in a modified triple test cross. Adjusted essential oil content (AdjEOC). C: control; MWD: moderate water deficit; SWD: severe water deficit.

3.2. Detection of Epistasis

Total epistasis was significant for SY, PODS, EOC, EOY, DSFAC, FAC, and FAY in C conditions, SY, EOC, EOY, DSFAC, HFAC, FAC, and FAY in MWD conditions, and SY, POSH, EOC, EOY, FAC, and FAY in SWD conditions (Table 2). The [i] type epistatic effect was detected for PODS in C and HFAC in MWD conditions.

For SY and EOC in MWD and SWD, DSFAC and FAC in C and MWD, and EOY and FAY in all irrigation regimes, [i] type epistasis was detected. The [j + l] type epistasis was observed for PODS and DSFAC in C, HFAC in MWD, and POSH in SWD conditions. For SY, [j + l] type epistasis was significant in all irrigation regimes. EOC, EOY, FAC, and FAY were significant in C and SWD conditions.

Table 2. Analysis of variance for the detection of epistasis for different traits in coriander under control (C), moderate water deficit (MWD), and severe water deficit (SWD) treatments.

Source of Variation	Mean Squares																	
	Epistasis			[i] Type Interaction			[j + l] Type Interaction			Epistasis × Replication			[i] Type × Replication			[j + l] Type × Replication		
	WT.	C	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD
d.f. Trait	6	6	6	1	1	1	5	5	5	12	12	12	2	2	2	10	10	10
SY	18.51 **	77.88 **	103.38 **	77.33 ^{ns}	434.63 **	551.08 **	6.82 **	6.52 *	13.81 **	3.51	2.11	0.32	16.77	2.71	0.31	0.91	1.93	0.20
PODS	1372.22 **	171.11 ^{ns}	231.27 ^{ns}	409.02 **	576.98 ^{ns}	472.32 ^{ns}	1564.89 **	89.91 ^{ns}	183.08 ^{ns}	111.60	126.45	113.48	4.96	131.09	123.63	1.54	125.54	111.39
POSH	21.26 ^{ns}	257.27 ^{ns}	911.63 **	10.04 ^{ns}	433.64 ^{ns}	343.26 ^{ns}	23.51 ^{ns}	221.93 ^{ns}	1025.37 **	8.41	147.22	114.25	5.01	157.28	98.27	9.56	85.28	117.42
EOC	0.01 **	0.06 **	0.04 *	0.008 ^{ns}	0.32 **	0.07 *	0.01 **	0.02 ^{ns}	0.03 *	0.002	0.005	0.01	0.0004	0.002	0.03	0.003	0.005	0.007
EOY	13.01 **	1.12 **	6.11 **	27.18 **	4.63 **	27.08 **	10.10 **	0.42 ^{ns}	1.86 *	0.20	0.10	0.62	0.20	0.11	0.90	0.20	0.11	0.62
DSFAC	1946.16 **	352.36 *	94.60 ^{ns}	8984.87 **	1607.40 **	0.10 ^{ns}	149.16 **	101.30 ^{ns}	113.53 ^{ns}	43.83	104.58	53.89	106.64	37.77	83.12	31.22	117.87	48.03
HFAC	1.32 ^{ns}	1.50 **	0.34 ^{ns}	0.05 ^{ns}	3.61 **	0.02 ^{ns}	1.55 ^{ns}	1.11 **	0.44 ^{ns}	0.52	0.002	0.21	0.02	0.0005	0.01	0.70	0.002	0.20
FAC	1962.58 **	329.77 *	198.41 *	9028.72 **	1458.08 **	0.05 ^{ns}	549.31 **	104.00 ^{ns}	238.10 *	43.85	104.59	54.20	107.47	37.53	83.44	31.18	117.99	48.48
FAY	12,322.17 **	12,667.25 *	84,002.48 **	38,567.90 **	71,297.22 **	385,980.70 **	7072.90 **	941.22 ^{ns}	23,606.77 **	1119.22	3167.17	1975.77	1119.29	2236.47	6378.73	1119.22	3353.23	1095.11

**, *, and ^{ns} are significant at the 0.01 and 0.05 level of probability and not significant, respectively. SY: seed yield; PODS: percent of dehulled seed; POSH: percent of seed hulls; EOC: essential oil content; EOY: essential oil yield; DSFAC: dehulled seed fatty acid content; HFAC: hull fatty acid content; FAC: fatty acid content; FAY: fatty acid yield.

The combined analysis of variance exhibited significant total epistasis \times WT interactions for all measured traits (Table 3). The [i] type \times WT interaction was significant for SY, PODS, DSFAC, HFAC, FAC, and FAY. The [j + l] type \times WT interaction was detected in all measured traits except SY.

Table 3. Analysis of variance for total, [i] type, and [j + l] type epistasis and their interactions with water treatments (WT) for different traits in coriander.

Source of Variation	Mean Squares					
	Epistasis	[i] Type Epistasis	[j + l] Type Epistasis	Epistasis \times WT	[i] Type \times WT	[j + l] Type \times WT
d.f. Trait	6	1	5	12	2	10
SY	225.82	145.86	241.81	152.42 **	187.23 **	19.88 ^{ns}
PODS	189.47	112.33	204.88	324.57 **	224.85 *	169.90 **
POSH	324.18	247.89	339.49	511.18 **	105.46 ^{ns}	367.11 **
EOC	211.99	199.67	214.47	355.82 **	41.82 ^{ns}	87.75 **
EOY	77.73	41.32	85.08	114.49 **	30.27 ^{ns}	36.56 **
DSFAC	2645.57	1365.48	2901.58	888.77 **	523.22 **	654.59 **
HFAC	3542.38	2888.86	3673.04	5124.36 **	2689.74 **	2153.34 **
FAC	4589.26	4122.39	4682.66	2158.28 **	2654.36 **	1458.27 **
FAY	11,1256.74	13,518.32	130,804.47	10,989.88 **	45,856.38 **	11,567.30 **

**, * and ^{ns} are significant at the 0.01 and 0.05 level of probability and not significant, respectively. SY: seed yield; PODS: percent of dehulled seed; POSH: percent of seed hulls; EOC: essential oil content; EOY: essential oil yield; DSFAC: dehulled seed fatty acid content; HFAC: hull fatty acid content; FAC: fatty acid content; FAY: fatty acid yield.

3.3. Additive and Dominance Components

The ANOVA for sums indicated that mean squares due to sums were significant for all the traits in C, MWD, and SWD conditions (Table 4). The sums \times WT interactions were significant for all measured traits except EOC, EOY, and HFAC (Table 5). The mean squares due to differences were significant for POSH, HFAC, FAY, and PODS in all water treatments and FAC and DSFAC in the MWD condition (Table 4). The differences \times WT interactions were significant for all measured traits except EOC (Table 5).

Table 4. Analysis of variance for additive and dominance components for different traits (within water treatments) in coriander under control (C), moderate water deficit (MWD), and severe water deficit (SWD) treatments.

Source of Variation	Mean Squares Due to											
	Additive Component						Dominance Component					
	Sums ($L_{1i} + L_{2i}$)			Sums \times Replication			Differences ($L_{1i} - L_{2i}$)			Difference \times Replication		
WT.	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD
d.f. Trait	5	5	5	10	10	10	5	5	5	10	10	10
SY	19.71 **	7.18 **	3.31 **	1.40	1.06	0.22	3.71 ^{ns}	0.31 ^{ns}	0.22 ^{ns}	1.30	0.20	0.21
PODS	980.85 **	1410.10 **	952.15 **	7.71	0.54	0.40	1631.00 **	322.97 **	118.96 **	3.53	0.20	0.43
POSH	881.43 **	1124.33 **	841.66 **	6.73	1.33	0.12	1423.24 **	258.22 **	241.45 **	5.11	2.23	0.70
EOC	0.08 **	0.04 **	0.05 **	0.01	0.003	0.007	0.003 ^{ns}	0.01 ^{ns}	0.01 ^{ns}	0.006	0.004	0.004
EOY	1.51 *	1.25 **	0.92 **	0.34	0.14	0.04	0.08 *	0.11 ^{ns}	0.20 ^{ns}	0.02	0.06	0.09
DSFAC	785.77 **	249.31 **	176.55 **	15.72	38.04	28.84	251.40 ^{ns}	121.68 *	81.86 ^{ns}	86.66	29.45	38.98
HFAC	12.64 **	14.34 **	14.74 **	0.004	0.001	0.001	0.63 **	0.71 **	0.62 **	0.004	0.001	0.003
FAC	719.49 **	173.96 *	150.19 *	15.73	38.03	28.73	248.95 ^{ns}	127.88 *	95.01 ^{ns}	86.47	29.41	38.66
FAY	8150.11 **	2863.10 *	1690.64 *	592.50	703.11	359.48	4449.79 *	907.07 **	431.90 *	861.96	78.48	116.85

**, *, and ^{ns} are significant at the 0.01 and 0.05 level of probability and not significant, respectively. SY: seed yield; PODS: percent of dehulled seed; POSH: percent of seed hulls; EOC: essential oil content; EOY: essential oil yield; DSFAC: dehulled seed fatty acid content; HFAC: hull fatty acid content; FAC: fatty acid content; FAY: fatty acid yield.

Table 5. Analysis of variance for additive and dominance components and their interactions with water treatments (WT) for different traits in coriander.

Source of Variation	Mean Squares					
	Additive Component			Dominance Component		
	Sum	Sum \times WT	Blocks (WT)	Difference	Difference \times WT	Blocks (WT)
d.f. Trait	5	10	30	5	10	30
SY	21.84 **	8.06 *	3.34	1.81 *	1.47 *	0.65
PODS	234.41 ^{ns}	6444.36 *	95.32	836.32 **	1002.51 **	183.25
POSH	562.36 **	789.35 **	121.32	697.45 **	793.11 **	148.36
EOC	0.07 ^{ns}	0.10 ^{ns}	0.05	0.01 ^{ns}	0.02 ^{ns}	0.01
EOY	1.04 ^{ns}	1.17 ^{ns}	0.63	0.16 *	0.23 **	0.05
DSFAC	452.85 **	558.45 **	88.63	236.41 *	367.77 **	78.92
HFAC	8.87 ^{ns}	10.23 ^{ns}	5.18	0.70 ^{ns}	1.12 **	0.35
FAC	698.11 **	878.32 **	149.85	187.35 *	287.21 **	65.23
FAY	6808.20 *	8947.05 **	2174.65	3663.13 **	1062.01 **	754.10

**, *, and ^{ns} are significant at 0.01 and 0.05 level of probability and not significant, respectively. SY: seed yield; PODS: percent of dehulled seed; POSH: percent of seed hulls; EOC: essential oil content; EOY: essential oil yield; DSFAC: dehulled seed fatty acid content; HFAC: hull fatty acid content; FAC: fatty acid content; FAY: fatty acid yield.

For traits not significantly affected by epistasis, the additive and dominance genetic components, direction of dominance, and degree of dominance were estimated (Table 6). Both additive and dominance genetic components were significant for PODS in MWD and SWD, HFAC in C and SWD, POSH in C and MWD, and DSFAC in SWD conditions. The average degree of dominance indicated that partial dominance was detected for PODS in MWD and SWD, HFAC in C and SWD, and DSFAC in SWD. Over-dominance was found for POSH in C conditions. The correlation between sums and differences were positive and significant for PODS in MWD and SWD and POSH in MWD, and negative and significant for HFAC in C and SWD conditions, indicating that the dominant genes have decreasing effects on the PODS and POSH traits and increasing effects on the HFAC. The positive but non-significant correlation for POSH in C showed that dominance was bidirectional, and alleles for lower and higher POSH were more or less equally distributed among the coriander populations examined. The estimates of heritabilities showed that POSH in C condition had relatively high broad-sense heritability ($h_B^2 = 0.72$) and low narrow-sense heritability ($h_N^2 = 0.20$). In the SWD treatment, PODS, HFAC, and DSFAC exhibited higher h_N^2 than in C. The average degree of dominance $[(H/D)^{1/2}]$ was less than unity for all these traits. It ranged from 0.16 for HFAC in MWD to 0.91 for POSH in C conditions.

The directions and relative magnitudes to recognize those genotypes which interacted with L_1 and L_2 to produce significant total epistasis for SY, PODS, POSH, EOC, EOY, DSFAC, HFAC, FAC, and FAY are presented in Table 7.

The genotypes TN-59-80 for PODS in C, EOC and EOY in SWD, and FAY in MWD, TN-59-160 for EOC in C and SWD, EOY in SWD, and FAY in C, TN-59-353 for SY in C and HFAC in MWD, TN-59-347 for SY, EOY, and FAY in C, POSH in SWD, EOC in C and SWD, DSFAC in MWD and FAC in MWD and SWD, TN-59-10 for SY in C, EOC in C and SWD, EOY in C and MWD, DSFAC and FAC in MWD, and commercial for POSH and EOC in SWD, EOY in C and MWD, and FAY in C conditions showed non-significant contributions towards total epistasis. The genotype TN-59-80 for SY in C and DSFAC in C and MWD as well as FAC in MWD and SWD conditions played an important negative and positive role, respectively. TN-59-160 for POSH in SWD, TN-59-353 for SY in MWD, EOY in C and SWD, and FAY in MWD and SWD, TN-59-347 for SY in SWD and EOY in MWD, and commercial for PODS in C, HFAC in MWD, and FAC in SWD accounted for

high negative proportions of the total epistasis. The genotypes TN-59-80 for DSFAC and FAC in C and MWD, TN-59-353 for POSH in SWD, EOC in all water treatments, and EOY in MWD, TN-59-347 for HFAC in MWD, and TN-59-10 for SY and FAY in C accounted for the maximum positive portion to the total epistasis.

Table 6. Estimates of components of variation and heritabilities for PODS, POSH, DSFAC, and HFAC under control (C), moderate water deficit (MWD), and severe water deficit (SWD) conditions.

Genetic Component	Estimates	WT.	PODS	POSH	DSFAC	HFAC
Additive variance (V_A)	(1/2) D	C	-	648.7 **	-	-
		MWD	939.6 **	939.6 **	-	9.6 **
		SWD	561.1 **	-	98.4 **	-
Dominance variance (V_D)	(1/4) H	C	-	542.5 **	-	-
		MWD	107.6 **	107.6 **	-	0.25 **
		SWD	117.5 **	-	14.3 **	-
Dominance ratio ($r_{s,d}$)	$(H/D)^{1/2}$	C	-	0.91	-	-
		MWD	0.34	0.33	-	0.16
		SWD	0.46	-	0.38	-
Narrow-sense heritability	V_A/V_P	C	-	0.54	-	-
		MWD	0.90	0.90	-	0.67
		SWD	0.82	-	0.56	-
Broad-sense heritability	V_G/V_P	C	-	0.90	-	-
		MWD	0.95	0.95	-	0.78
		SWD	0.88	-	0.64	-

** ns is significant at 0.01 level of probability. PODS: percent of dehulled seed; POSH: percent of seed hulls; DSFAC: dehulled seed fatty acid content; HFAC: hull fatty acid content.

Table 7. Epistatic deviations of individual coriander genotypes SY, EOY, and FAY exhibiting significant differences among genotypes tested under control (C), moderate water deficit (MWD), and severe water deficit (SWD) conditions.

Genotypes	SY			PODS			POSH			EOC			EOY		
	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD
TN-59-80	-3.20 *	-3.23 **	-4.48 **	0.67 ns	-	-	-	-	24.77 **	-0.05 **	0.06 **	0.05 ns	-0.81 **	-0.69 **	-0.68 ns
TN-59-160	-3.10 *	-4.55 **	-4.73 **	-13.13 **	-	-	-	-	-12.30 **	-0.01 ns	0.08 **	0.06 ns	-0.76 *	-0.62 **	-0.78 ns
TN-59-353	-2.33 ns	-6.87 **	-4.67 **	-2.37 **	-	-	-	-	28.57 **	0.14 **	0.28 **	0.28 **	-4.94 **	0.61 **	-1.96 **
TN-59-347	-1.90 ns	-5.17 **	-9.90 **	13.17 **	-	-	-	-	-2.63 ns	-0.02 ns	0.08 **	-0.03 ns	-0.37 ns	-1.01 **	-1.54 **
TN-59-10	0.83 ns	-4.82 **	-4.62 **	46.23 **	-	-	-	-	-8.60 **	0.01 ns	0.13 **	0.01 ns	-0.20 ns	-0.31 ns	-1.06 *
Commercial	-2.73 *	-4.05 **	-4.80 **	-15.97 **	-	-	-	-	0.93 ns	0.05 **	0.07 **	0.01 ns	-0.26 ns	-0.40 ns	-0.92 *
Genotypes	DSFAC			HFAC			FAC			FAY					
	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD	C	MWD	SWD			
TN-59-80	42.30 **	20.44 **	-	-	0.44 **	-	43.25 **	20.00 **	12.33 **	62.53 **	-33.40 ns	-75.78 *			
TN-59-160	21.39 **	9.60 **	-	-	0.94 **	-	20.79 **	8.67 **	-5.67 **	27.56 ns	-55.57 ns	-126.80 **			
TN-59-353	34.82 **	7.67 **	-	-	0.01 ns	-	34.29 **	7.67 **	7.67 **	92.46 **	-177.00 **	-322.20 **			
TN-59-347	13.89 **	5.39 ns	-	-	1.39 **	-	13.62 **	4.00 ns	2.00 ns	33.00 ns	-80.30 *	-135.82 **			
TN-59-10	12.47 **	4.12 ns	-	-	0.12 **	-	13.43 **	4.00 ns	-6.00 **	95.90 **	-71.28 *	-100.08 **			
Commercial	9.17 **	9.47 **	-	-	-0.19 **	-	9.01 **	9.67 **	-10.67 **	-33.73 ns	-58.33 *	-117.93 **			

**, *, and ns are significant at 0.01 and 0.05 level of probability and not significant, respectively. SY: seed yield; PODS: percent of dehulled seed; POSH: percent of seed hulls; EOC: essential oil content; EOY: essential oil yield; DSFAC: dehulled seed fatty acid content; HFAC: hulls fatty acid content; FAC: fatty acid content; FAY: fatty acid yield.

4. Discussion

Drought is a serious worldwide problem, influencing crop production and quality. Recent global climate change has made this situation more serious [34]. When plants are exposed to restricted environmental conditions, the production of some biochemical products, such as essential oils, can be improved [35]. However, there are reports on

the negative effect of environmental constraints on other products such as SY, FAC, and FAY [8,9,32]. Therefore, the present study was undertaken to investigate the nature of the genetic controlling response of coriander to different irrigation regimes for SY, PODS, POSH, EOC, EOY, DSFAC, HFAC, FAC, and FAY.

Most of the multiple mating designs used to estimate the genetic architecture of polygenic characters assume epistasis to be absent or of little importance, and most genetic models rarely provide a reliable estimation of this assumption. Several studies in various plants using the triple test cross model have shown that epistasis is a significant component of genetic variability for polygenic traits [18–20,23,24,36].

4.1. Seed Yield

The SY was affected by water stress, indicating that the expression of SY depends on non-allelic interactions and that these three irrigation regimes differed in the expression of epistasis. Furthermore, epistasis \times WT interactions were significant and therefore so was the sensitivity or non-consistent performance of epistasis of the SY-related loci between irrigation regimes. It is remarkable that interactions with water treatments depend on the number of loci involved in trait inheritance, i.e., the higher the number of involved loci, the greater the possibility of an environmental influence on trait expression, which is characteristic of quantitative traits. Furthermore, mechanisms involved in the expression of SY may differ according to the water treatments. Thus, if the loci that determine SY in coriander participate in adaptation and interact with the particular irrigation regimes, then epistasis will be environmentally variable, and this could therefore be a possible explanation for the strong epistasis \times WT interaction detected in this study.

Changes in the relative magnitudes of the epistatic gene effects (total, i type and $j + l$ type) between different water treatments can occur if the loci that determine the trait have different sensitivities for the water treatments considered [29]. In agreement with our results, Upadhyaya and Nigam [17] in peanut, Sood et al. [18] in linseed, Wolf and Hallauer [37] in maize, Khattak et al. [25] in mungbean, and Barona et al. [20] in soybean reported a similar instability of epistatic gene effects. As Pooni and Jinks [38] stated, [i] type epistatic gene effects are more sensitive to environmental differences than the other two types. According to the results, the [i] type of interactions were predominant as compared to the [$j + l$] type for SY in MWD and SWD. In the breeding program, where the purpose was to develop inbred lines, the [i] type interactions were possibly the most important because they are a fixable and linear directional component in homozygous genotypes, contributing to the superiority of elite lines [39].

4.2. Fatty Acid Content

Variable FAC in different parts of coriander was detected, with values of 9.3% in hulls and 22.65% in de-hulled seeds by Sriti et al. [40], and 17.6% and 37.60% in whole seed and e-hulled seeds, respectively, by Evangelista et al. [4]. Thus, the results of the present study are in a similar range to those found in previous reports. It was reported that water deficit led to a reduction in FAC in coriander [32] and cumin [7,13] as water stress increased, whereas in the present study genotypes showed different levels of FAC in different irrigation regimes.

Additive \times additive epistatic effects were found to control (in part) the expression of FAC, DSFAC, FAY, and HFAC in C and MWD when these and the SWD treatment data were analysed together. The presence of [i] type epistasis \times WT interactions indicated that breeding for DSFAC, HFAC, FAC, and FAY should be done in water conditions relevant to the target environment. The absence of significant [$j + l$] type epistasis for FAC, FAY and DSFAC in MWD indicated that additive \times dominance and dominance \times dominance types of interactions between controlling genes were either not present or of relatively smaller magnitude. Furthermore, results indicated that the relative magnitude of the [$j + l$] type of interaction was greater than the [i] type in SWD. Epistasis of the [$j + l$] type can be used in the presence of the development of hybrids [41]. Studies on genetic variation in

coriander using diallel mating designs showed that dominant gene action is involved in the inheritance of FAY [32].

4.3. Essential Oil Content

Results revealed that EOC was affected by water deficit, in accordance with Bettaieb et al. [12] in *Salvia officinalis* and Alinian [10] in cumin and coriander [42]. Furthermore, water stress affected the EOC by PODE, indirectly, which is obvious from the difference between EOC and AdjEOC. Results indicated that the [i] types of interactions were predominant as compared to the [j + l] type for EOC in MWD and SWD, and EOY in all water treatments. Consequently, we suggest postponing the selection for EOC to later generations of inbreeding (F_5 or F_6) to exploit the beneficial effects of [i] type of epistasis.

4.4. Epistatic Deviations of Individual Coriander Genotypes

Overall, the six genotypes (TN-59-10, TN-59-80, TN-59-160, TN-59-353, TN-59-347, and commercial) contributed significantly towards the epistatic deviations, indicating that the presence of non-allelic interactions are determined to some extent by the genotypes included in the triple test cross design along with L_1 and L_2 testers. Therefore, this reinforces the need to include several genotypes in studies designed for the detection of non-allelic interactions and to estimate dominance and additive components of variation with equal precision through the TTC method [25,27].

In this study, extreme high vs. low testers (TN-59-158 and TN-59-230) indicated high efficiency in detecting epistasis for most traits. The experimental sample size necessary to detect allelic interactions through the triple test cross depends largely on the gene dispersion between testers [38]. However, the use of more pairs of testers and additional environments could have improved the possibility of detection of non-allelic interactions, especially for the traits which were not detected in this experiment. Several studies have reported that the manifestation of non-allelic interactions in crops occurs in diverse genotypes and is tester-dependent [22,36,43].

Since the epistasis effect was significant for traits in different water treatments, the estimates of additive and dominance components of genetic variation for these traits were biased to an unknown extent. Therefore, for given traits, additive and dominance variance components were estimated for each water treatment only if non-allelic interactions were not detected.

The higher magnitude of additive variance, as found in DSFAC and HFAC in SWD and MWD, respectively, is indicative of the relative importance of fixable types of gene action for these traits. The preponderance of additive components for DSFAC and HFAC is contrary the findings of earlier studies, where the preponderance of the dominance component for DSFAC and HFAC by a diallel mating design was reported [32].

Water deficit led to a greater decrease in PODS than POSH, which indirectly affects the whole-seed essential oil and fatty acid content. Furthermore, as discussed previously, seed de-hulling reduces the amount of material to be processed and can help to prevent considerable oil absorption by hulls in the oil-pressing extraction system [4]. The genetic control mechanism of POSH was affected by water stress and the proportion of dominance gene action decreased as water stress progressed. The genetic control of PODS was governed by partial dominance gene action in MWD and SWD water conditions because $[(H/D)^{1/2}]$ was between 0.34 and 0.46 and h_B^2 was less than 0.20 in both water treatments.

Dominance variance estimated by the triple test cross method refers to different alleles between the two testers [44]. Meanwhile, if the number of those alleles is less than that of total number of segregating alleles in the population for expression of this trait, the dominance variance component will be underestimated [17]. In general, the significance of the differences in mean squares indicates that dominant gene action plays a key role in the genetic control of a given trait. Furthermore, it is specified that under the same conditions, the estimates of the additive variance component could include a portion due to dominance deviations and therefore could be biased upward [44]. Thus, in the

absence of the dominance variance component, the significance of the sum mean squares provides an accurate estimate of the presence of additive variance regardless of dominance contamination and the number of alleles which differ between L_1 and L_2 .

The estimation of narrow and broad-sense heritability from the analysis of the triple test cross is uncommon because the testers are two high and low extreme selection genotypes and would not predict the response to selection [24]. However, Khan and McNeilly [23] in maize, Pooni et al. [45] in rice, and Devey et al. [46] in *Lolium* estimated heritability from the triple test cross method, but its value was insignificant.

As discussed previously, to obtain unbiased estimates of genetic components of variance, the two testers should be extremely low vs. high for a character under consideration. However, when multi traits are considered together, achieving this purpose is not easy. Hence, the result of the present study can be considered as a tool for understanding the types of genetic control mechanisms in the involved coriander traits, rather than a tool for obtaining more realistic components of genetic variation.

5. Conclusions

Overall, the highly significant [i] type epistasis \times WT, [j + l] type epistasis \times WT, sums \times WT, and differences \times WT effects for measured traits suggest that different breeding strategies may be adopted in different conditions that are representative of the target environment for breeding. In the cases where [i] type epistasis was detected across water treatments we suggest postponing the selection for advanced generations and the maintenance of large segregating populations for selection to allow combinations of favorable alleles to occur for exploitation. The results also indicate the importance of dominance variance and [j + l] type epistasis in POSH and HFAC. Due to their non-directional and unfixable nature, dominance and [j + l] type epistasis can be exploited through heterosis breeding by developing hybrids. For open-pollinated plants and coriander with low inbreeding depression, breeding procedures are available for the exploitation of existing linear and non-directional components of genetic components in coriander via the development of homozygous lines and hybrid varieties, respectively.

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