

Inheritance mechanism of fruit yield and yield-related traits in tomato for cadmium stress tolerance

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Abstract: Understanding inheritance patterns and yield-related traits under cadmium stress is essential for breeding strategies that reduce cadmium's negative effects on crops. In a study, fifteen F1 tomato hybrids from six genotypes were evaluated under both cadmium and non-cadmium conditions. The genetic analysis confirmed that a simple additive-dominance model explained the inheritance of most traits, suggesting that a few genes, often with one having a stronger effect, control these traits. Over-dominance was observed in most traits, and genotypes P3 and P5 carried the most dominant genes, performing best under cadmium stress. Heritability estimates showed that, under non-cadmium conditions, traits like branch number, fruit set, fruit mass, and locule number had medium narrow sense heritability, indicating dominance gene action was the main factor in inheritance. Other traits with low heritability also pointed to the importance of dominance effects. As a result, P3 and P5 genotypes were more tolerant to cadmium stress due to their dominant gene composition. Understanding the roles of dominance and non-additive gene action can guide the development of high-yield, cadmium-tolerant tomato varieties.

Key words: Average degree of dominance, Cd stressed, gene action, heritability, *Solanum lycopersicum* L., variance/covariance graphs

Mehanizmi dedovanja tolerance na kadmijev stres pri pridelku plodov in z njim povezanih lastnosti pri paradižniku

Izvleček: Razumevanje vzorcev dedovanja na s pridelkom povezane lastnosti v razmerah kadmijevega stresa je ključno pri strategijah zlahtnjenja, ki zmanjšujejo negativni učinek tega stresa na gojene rastline. V raziskavi je bilo ovrednoteno petnajst F1 hibridov paradižnika vzgojenih iz šest genotipov v razmerah z in brez kadmijevega stresa. Genetska analiza je potrdila, da je model preproste aditivne dominancije pojasnil dedovanje večine lastnosti, kar nakazuje, da le redki geni, od katerih imajo nekateri močan učinek, nadzorujejo večino teh lastnosti. Prekomerna prevlada je bila opažena pri večini lastnosti, genotipa P3 in P5 sta imela najbolj dominantne gene, ki so se izražali najboljše v razmerah kadmijevega stresa. Ocene dednosti so pokazale, da imajo v razmerah brez kadmijevega stresa lastnosti kot so število stranskih poganjkov, nastavki plodov, masa plodov in število lokusov srednje pomensko dednost, kar kaže, da je delovanje dominantnih genov glavni dejavnik pri dednosti. Lastnosti z majhno dednostjo so tudi nakazale pomen učinka dominancije. Kot rezultat sta se izkazala genotipa P3 in P5 kot bolj tolerantna na kadmijev stres zaradi vsebovanja dominantnih genov. Razumevanje pomena dominancije in ne aditivnega delovanja genov lahko vodi v razvoj sort z velikim pridelkom in toleranco na kadmijev stres.

Ključne besede: poprečna stopnja dominancije, Cd stress, delovanje gena, dednost, *Solanum lycopersicum* L., grafi varianc in kovariance

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1 INTRODUCTION

Cadmium is among the heavy metal pollutants known to its adverse effects on plant growth and development (Zhang *et al.*, 2019; Li *et al.*, 2023). Cadmium pollution has shown a continually increasing trend due to anthropogenic activities relating to mining and smelting. Even though cadmium, in nature, is present at low concentration levels, the recent industrial expansion activities and phosphate fertilizers containing cadmium have contributed immensely to environmental alteration. Cadmium at high concentrations in soils causes substantial damage to plants. Symptoms include yellowing of leaves, reduction of root growth and photosynthesis (Alcántara *et al.*, 1994; Zhang *et al.*, 2014; Chiao *et al.*, 2020; Zhao *et al.*, 2021). Cadmium stress has been shown to induce the regulation of various metabolic pathways in the case of tomato plants. This could be a basis to genetically improve cadmium tolerance (Chen *et al.*, 2023). Cadmium accumulation in soil and tomato plants leads to a range of morphological, physiological, biochemical, and molecular changes, often resulting in reduced plant growth, biomass, and photosynthetic capacity, as well as increased oxidative stress and activation of antioxidant defenses (Badawy *et al.*, 2022; Sarwar *et al.*, 2023; Huang *et al.*, 2024). Glutathione increases the tolerance of tomatoes to cadmium stress through the promotion of chelation and sequestration and the stimulation of nitric oxide, S-nitrosothiols, and the antioxidant system via a redox-dependent mechanism (Hasan *et al.*, 2016).

The tomato is one of the economically important vegetables grown globally. Hence, the genetic basis for the agronomic traits regarding plant height, branching, fruit set, fruit mass, fruit yield, number of locules, flesh thickness, and total soluble solids under cadmium stress response should be considered important in the program of developing cadmium stress-tolerant varieties (Bhattarai *et al.*, 2018; Guo *et al.*, 2022). In addition, estimating the magnitudes of abiotic stresses like cadmium toxicity, which may affect heritability and the mode of gene action in such traits, is important for developing cadmium-stress-tolerant tomato varieties (Zhang *et al.*, 2019). Moreover, the study by Xian *et al.* (2023) suggests that the results on heritability and gene action of agronomical traits should be used to update breeding strategies for tomato cultivars to perform well under normal and cadmium-stressed conditions. The genetic mechanisms governing cadmium tolerance in crops have been studied by Jalmi *et al.* (2018), but further research is needed to understand the intricate regulatory networks that govern this tolerance, as noted by Silva and Oliveira (2014). Furthermore, Lupp *et al.* (2024) noticed that USP163 can be utilized in breeding programs aiming to cultivate geno-

types with high Cd tolerance, indicating its potential for effective breeding strategies.

Therefore, the study aimed to investigate the inheritance pattern of fruit yield and related traits in tomato under Cd stress to maintain these traits and breed Cd-tolerant, high-yielding cultivars.

2 MATERIALS AND METHODS

A greenhouse experiment was conducted in a plastic greenhouse on tomato plants (*Solanum lycopersicum* L.) located at Sharqia Governorate, Egypt, in seasons 2021/2022 and 2022/2023. Six superior genotypes were selected for crossing, 'Super Marmande' (P1), 'Pearson Imp' (P2), 'Tan Shit Sta' (P3), 'Castle Rock' (P4), 'Peto Mech' (P5), and 'Edkawy' (P6). In the first season, 15 F₁ hybrids were obtained by crossing parents using a 6 x 6 half-diallel mating method. In the second season, parents and F₁ hybrids were evaluated in two randomized complete block design experiments with three replications. One experiment involved a Cd stress treatment, where 30 ppm cadmium ion liter⁻¹ of water (475 liter ha⁻¹) was sprayed at the flowering stage, while the other experiment was a control sprayed with pure water.

Two adjacent experiments were laid out in a randomized complete block design, with three replications for each treatment. Irrigation in the field was done through drip irrigation; plants were 50 cm apart on rows, and one bed measuring 1.5 meters in width and 8 meters in length had two lines of drippers. The transplantation process was done on the 1st of November, 2022. The experimental soil used was sandy loam, with a pH value of 8.0 and an EC of 1.15 dSm⁻¹. It is, however, worth noting that during the experiment, the irrigation water used had a relatively lower value of EC at 1.88 dSm⁻¹ with a pH of 7.37. The production of tomatoes in the plastic greenhouse was done by following all the recommended guidelines for agriculture practices.

Ten plants were randomly selected to record the data on plant height in cm and the number of branches per plant. For calculating the percentage of fruit set, the average number of the first four clusters was calculated. Fruit average mass (g) was calculated by total yield/total number of fruits. Fruit yield per plant (kg) was determined by summing the mass of all fruits for each single plant. The number of locules per fruit was measured at random in five ripe fruits, and the total soluble solids (T.S.S) present in ripe fruits were assessed using a hand refractometer, following the method of AOAC. (1990). Fruit flesh thickness (mm) was measured throughout the harvesting process using vernier calipers.

2.1 STATISTICAL ANALYSIS

Variance analysis for each treatment was carried out as described by Steel et al. (1997). The genetic statistical analyses were conducted, using modified Hayman analysis of variance as per Hayman's (1954a) method, as modified by Jones (1965). Variance/covariance (V_r/W_r) graphs for each trait were prepared according to (Jinks, 1954), in order to determine the frequency of dominant and recessive alleles in parental tomato genotypes at two treatments, while the genetic components along with respective genetic parameters were estimated according to (Hayman, 1954b). Estimates of the standard error for the genetic parameters D , H_1 , H_2 and F were provided by using (Hayman, 1954b) covariance matrix, in which the variance ratio F was used to test the statistical equality i. e. variances homogeneity for gene action of additive, non-additive types and mean square error. These parameters provided estimates of the following ratios:

These parameters provided estimates of the following ratios:

- 1. Measure of average degree of dominance over all loci defined as $(H_1/D)^{1/2}$.
- 2. $(H_2/4H_1)$ represents the measure of the mean value of the product u and v , which represent frequencies of positive and negative alleles respectively, in parents. It has a maximum value of 0.25 when $p = q = 1/2$.
- 3. The ratio of the total number of dominant to recessive genes in all of the parents is defined as K_D/K_R .

3 RESULTS AND DISCUSSION

3.1 MORLEY JONES ANOVA

While the additive component, therefore, employs the effect of every gene within an individual genotype toward a trait, dominance is the interaction between different alleles at the same gene locus. Studies dealing with the balance between additive and dominance effects help geneticists understand how complex traits are passed on to succeeding generations. This can be utilized in breeding programs for the advancement of crop characters through the improvement of the overall genetic composition of the genotypes. Thus, the variance study revealed that all studied traits under both conditions showed significant components 'a' additive and 'b' dominance, as represented in Table 1. This explained very well the importance of both genetic components for the inheritance of the traits and the authenticity of further V_r - W_r graph analysis (Goffar et al., 2016).

These components had a mean sum of squares which was up to highly significant, therefore, making both very important in the inheritance of those traits. Estimated significant additive and dominant variances in heavy metal tolerance in tomato plants; dominant gene action was more prevalence over additive variance (Raja et al., 2022). Unidirectional dominance in the hybrids (b_1) for the above two conditions is presented in Table 1. Highly significant differences were observed in plant height, branches, fruit set, fruit mass, fruit yield, locules, flesh thickness, and total soluble solids. This indicating thereby that one of the parents contributed mainly to these characters. Hence, hybrid breeding has a potential role in improving fruit quality and yield, leading to the development of superior varieties with increased productivity and market value (Lone et al., 2021). The asymmetrical distribution of the gene under both conditions presented in Table 1 was highly significant for all studied traits.

This pointed out that some genes were more influential in determining a particular trait, and investigating the possibility of interaction between such genes could unveil useful information about the underlying genetic caused that attribute to variation in traits. Significant residual dominance effects in individual crosses under both conditions for all studied traits are given in Table 1. This indicated that some genetic combinations persisted to always give higher magnitudes of dominance for such traits. These effects, therefore, suggested that specific alleles were more dominant when combined and hence give more pronounced effects on phenotype (ELnager, 2018). These were constant in all the crosses studied in tomato, therefore showing which genetic combinations were more dominant when paired together.

3.2 V_r - W_r GRAPH

A graphical variance/covariance analysis presented in Figs. 1–8 seemed to provide a lot of information concerning the genetic situation and adequacy of the additive/dominance model of gene action. The V_r - W_r statistical analysis showed that all studied traits under both conditions meet the assumptions of the simple additive-dominance genetic model (Table 2), which indicated further genetic component determination. The graph of points of parental genotypes for the studied traits was distributed in a wide area, reflecting significant genetic diversity among the tested parents (Kumar et al., 2020). In addition, non-significance of the test t^2 indicated validation for the use of the simple additive dominance model for genetic analysis across all studied traits under both conditions, as shown in Table 1. The results indi-

Table 1: Hayman analysis of variance following Morley Jones modification for fruit yield and yield-related traits under non-Cd stressed and Cd stressed conditions

S.O.V	d.f.	Plant height		Branches plant ⁻¹		Fruit set		Fruit mass	
		NCS	CS	NCS	CS	NCS	CS	NCS	CS
a	5	23.59**	14.17**	1.57**	0.94**	161.96**	38.33**	131.30**	36.61**
b1	1	231.22**	176.54**	3.59**	7.60**	1250.04**	574.35**	788.77**	774.22**
b2	5	6.63**	9.43*	0.87**	0.22	165.83**	55.25**	85.03**	30.39**
b3	9	7.44**	7.11	0.17	0.39	20.64**	50.04**	9.93	10.08*
b	15	22.09**	19.18**	0.63**	0.82**	151.00**	86.73**	86.88**	67.79**
Total	20	22.46**	17.92**	0.87**	0.85**	153.74**	74.63**	97.99**	59.99**
S.O.V	d.f.	Fruit yield Plant ⁻¹		Locules Fruit ⁻¹		Flesh thickness		Total soluble solids	
		NCS	CS	NCS	CS	NCS	CS	NCS	CS
a	5	0.40**	0.24**	0.69**	0.25**	0.56**	0.41**	0.49**	0.29**
b1	1	5.09**	3.14**	3.26**	2.47**	5.94**	2.41**	6.25**	2.19**
b2	5	0.17**	0.10*	0.18**	0.22**	0.12**	0.29**	0.17**	0.31**
b3	9	0.07*	0.10*	0.18**	0.33**	0.36**	0.24**	0.34**	0.37**
B	15	0.44**	0.30**	0.38**	0.44**	0.65**	0.40**	0.68**	0.47**
Total	20	0.43**	0.29**	0.46**	0.39**	0.63**	0.40**	0.63**	0.43**

Where: S.O.V = Source of variation; Df = Degrees of freedom; NCS = Non-Cd stressed; CS = Cd stressed; a = additive effects; b1 = directional dominance; b2 = asymmetry of allele frequencies among parents; b3 = residual dominance deviations; b = total dominance component. * and ** indicate significance at the 5 % and 1 % probability levels, respectively.

Table 2: Adequacy test of the data for additive-dominance model for fruit yield and yield-related traits under non-Cd stressed (NCS) and Cd stressed conditions (CS)

Traits		t ²	Joint regression analysis			Analysis of variance of array	
			(b) ± SE	b = 0	b = 1	Wr + Vr	Wr - Vr
Plant height	NCS	2.75	0.58 ± 0.17	3.44*	2.53	3340.74*	841.59**
	CS	2.45	0.36 ± 0.22	1.67	2.94*	2122.69*	926.85**
Branches plant ⁻¹	NCS	0.03	0.70 ± 0.32	2.20	0.96	4.56**	1.05**
	CS	0.49	0.69 ± 0.23	3.01*	1.37	8.30*	2.07**
Fruit set	NCS	1.96	0.54 ± 0.20	2.70	2.34	69123.73**	44588.91**
	CS	2.76	0.54 ± 0.18	3.02*	2.62	26198.10**	13886.87**
Fruit mass	NCS	1.99	0.75 ± 0.13	5.69**	1.92	40514.18**	13017.24**
	CS	1.90	0.20 ± 0.25	0.78	3.15*	11924.21**	10166.35**
Fruit yield Plant ⁻¹	NCS	1.20	0.73 ± 0.16	4.48*	1.64	1.00**	0.27**
	CS	2.56	0.42 ± 0.20	2.08	2.82*	0.44**	0.21**
Locules Fruit ⁻¹	NCS	1.61	0.62 ± 0.19	3.34*	2.02	1.04**	0.15**
	CS	2.27	0.34 ± 0.23	1.50	2.92*	0.93**	0.41**
Flesh thickness	NCS	2.67	0.50 ± 0.19	2.65	2.68	1.97**	0.65**
	CS	0.74	0.14 ± 0.32	0.44	2.64	1.27**	0.76**
Total soluble solids	NCS	0.02	0.61 ± 0.36	1.68	1.09	1.40**	0.62**
	CS	2.68	0.07 ± 0.24	0.30	3.94*	1.40**	0.83**

Where: NCS = Non-Cd stressed; CS = Cd stressed; t² = t-test for adequacy of the additive-dominance model; b = regression coefficient of Wr on Vr ± standard error (SE); b = 0 and b = 1 = t-tests for deviation of b from zero and unity, respectively; Wr + Vr = test for environmental effects; Wr - Vr = test for the presence of non-allelic (epistatic) interactions. * and ** indicate significance at the 5 % and 1 % probability levels, respectively.

cated that the observed genetic effects were mainly due to additive and dominant gene actions rather than gene interactions. This suggested that the studied traits were most likely controlled by a few major genes exhibiting additive and dominant effects, making them good candidates for further genetic mapping and marker-assisted selection within breeding programs (Bhandari et al., 2023). These findings provide important insights into the genetic architecture of these traits and, in turn, bring promising opportunities for improving breeding strategies in the future. Therefore, the traits studied at this point have met the assumptions of the model, and further, the Vr-Wr graph and Hayman's numerical approach will be evaluated.

3.3 AVERAGE DEGREE OF DOMINANCE

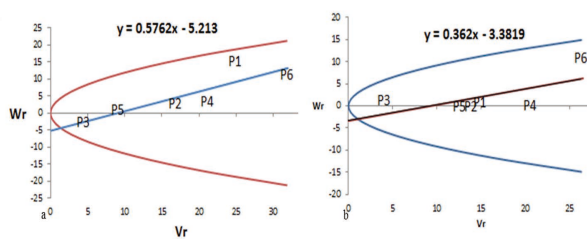


Fig 1: vr-wr graph for plant height (a) under non-cd stressed and (b) under cd stressed conditions

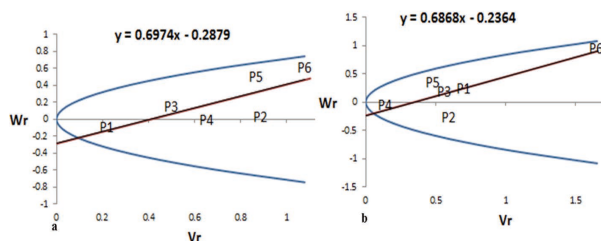


Fig 2: vr-wr graph for branches plant⁻¹ (a) under non-cd stressed and (b) under cd stressed conditions

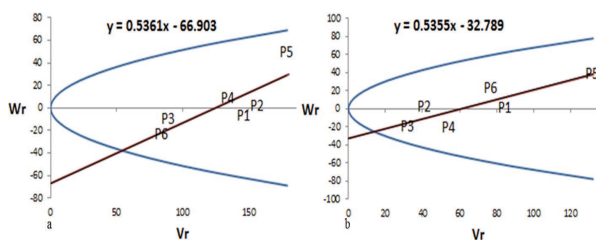


Fig 3: vr-wr graph for fruit set (a) under non-cd stressed and (b) under cd stressed conditions

The graph provided an information point that was quantified through the average level of dominance, assessed by the departure from the origin of the point at which the regression line cuts the Wr axis. Considering this, it could be clearly noticed that the inheritance of flesh thickness exhibited partial dominance (Fig. 7a) and total soluble solids (Fig. 8a) under non-Cd stressed conditions. The regression lines intercepting the Wr-axis above the origin, with the values of 0.0149 and 0.0275, respectively, indicated that these characters were controlled by polygenes, with one gene having stronger effect than the other. Furthermore, the partial dominance represented here suggested that the heterozygous individuals express an intermediate phenotype rather than the homozygous individuals. In contrast, this representation presented over-dominance in the inheritance under both conditions, as the regression lines intercepted the Wr-axis below the origin with negative values for 'a' (Rudas and Torbaniuk, 2025). These values were 5.213 and -3.3819 for plant height, 0.2879 and -0.2364 for branches, 66.903 and -32.789 for fruit set, 39.051 and -6.3843 for fruit mass, 0.1762 and -0.0531 for fruit yield, 0.0702 and -0.0904 for locules, under non-Cd and Cd -stressed conditions, respectively, along with -0.1437 for flesh thickness and -0.2232 for total soluble solids under non-cd stressed. This meant that the dominant gene alleles in the tomatoes belied the expression of some traits and pointed toward gene interaction or epistasis in their inheritance.

Many of these traits were primarily controlled by dominant alleles, and it did hint that an allele had the larger effect on the phenotype, the more likely it was to be dominant. This supported the hypothesis that alleles having a larger effect on phenotype are more likely to be dominant in tomato breeding (Mukherjee et al., 2024). In this regard, Patel and Kathiria (2018) noted the existence both of partial and complete dominance in chilli traits, with over-dominance has also been observed for variables like fruits per plant, pedicel length, seeds per fruit, and 100 seed mass.

3.4 THE DISTRIBUTION OF DOMINANT AND RECESSIVE GENES AMONG PARENTS

The distribution of dominant and recessive genes among parents was carried out by the order of array points along the regression line. The points closest to the origin in this ordering were those of parents bearing the most dominant genes, whereas those with the most recessive genes fell further from the origin. It is possible to elucidate the genetic makeup of parental genotypes by ordering an array along the regression line (Mukherjee et al., 2024).

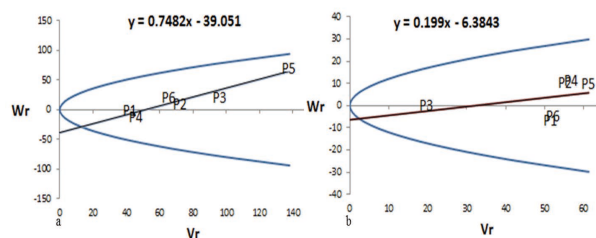


Fig 4: vr-wr graph for fruit mass (a) under non-cd stressed and (b) under cd stressed conditions

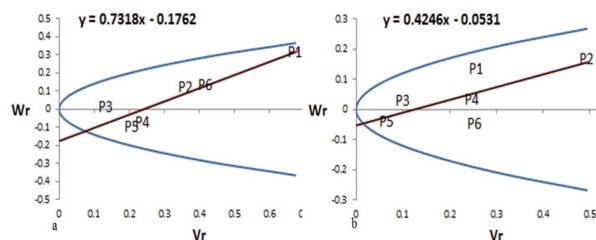


Fig 5: vr-wr graph for fruit yield plant⁻¹ (a) under non-cd stressed and (b) under cd stressed conditions

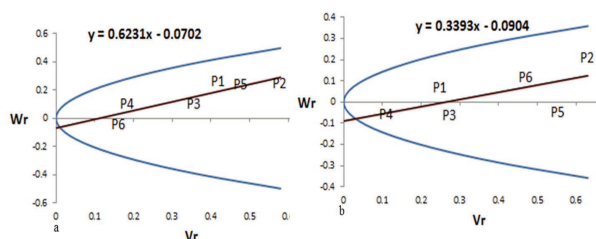


Fig 6: vr-wr graph for locules fruit⁻¹ (a) under non-cd stressed and (b) under cd stressed conditions

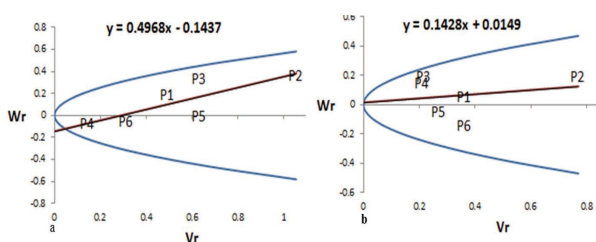


Fig 7: vr-wr graph for flesh thickness (a) under non-cd stressed and (b) under cd stressed conditions

Parent P3 had more dominant genes and therefore should have shown more consistent and uniform growth. In contrast, parent P6 showed a higher frequency of the recessive genes concerned with plant height under both experimental conditions. The dominant genes of P3 most probably contributed to the uniformity and consistency of its genetic profile, whereas P6 might show more vari-

ability concerning plant height because of its recessive genes. Hence, the genetic profile of P3 will show signs of uniqueness and a possible impact on the variation in plant height.

The high concentration of the dominant genes could be because of the presence of such genes in their genetic code, predominantly observed in P1 under non-Cd stressed conditions and P4 under Cd stressed conditions. On the contrary, P6 represented a higher preponderance of recessive genes across both conditions, which could be based on a potential influence on the genetic make-up of the branches.

As for the fruit set, it was observed that the dominant genes mostly prevail in the P6 and P3 under non-Cd stressed and P3 and P2 under Cd stressed conditions. In contrast, the recessive genes were more prevalent in the P5 across both conditions. The most probable reason is that these genes are included in their genetic code. Moreover, it gives an overview of how these genes work regarding fruit growth and development.

Frequency of dominant genes in fruit mass was expressed higher under non-Cd stressed conditions, especially in P1 and P4, while in Cd-stressed conditions, P3 was dominant. Conversely, a greater expression of recessive genes was observed in P5 under both conditions. This could be due to their possession of these genes in their genetic code.

It could be clearly noticed that dominant genes were more frequent in P3 concerning the fruit yield under non-Cd stressed conditions and P3 and P5 under Cd stressed conditions. On the other hand, recessive genes had higher frequencies in P1 under non-Cd stressed conditions and P2 under Cd stressed conditions. This may be due to the presence of such genes in their genetic code.

Dominant genes in P4 and P6 were more prevalent in the locules under non-Cd-stressed conditions and P4 in plants under Cd stressed conditions. Conversely, the expression of recessive genes was more pronounced in P2 across both experimental conditions. Since it was contained in the genetic makeup, this variation must have emanated from it. Thus, plant genetic composition

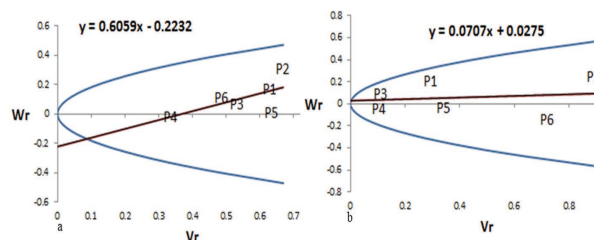


Fig 8: vr-wr graph for total soluble solids (a) under non-cd stressed and (b) under cd stressed conditions

counted much in the determination of the parental genotype composition.

The dominance in the genetic composition regarding the flesh thickness and total soluble solids was particularly evident in the dominant genes under both conditions, especially P4 under non-Cd stressed and P4 and P3 under Cd-stressed condition. In contrast, the P2 showed a higher trend in the prevalence of recessive genes under both conditions, potentially impacting the genetic makeup of flesh thickness and total soluble solid traits. In this regard, Sappah et al. (2021) demonstrated that the MTP genes of tomato are differentially expressed and play important roles in processes related to metals; SIMTP1, SIMTP3, SIMTP4, SIMTP8, SIMTP10, and SIMTP11 showed the highest expression response to heavy metal stress. Additionally, Raja et al.

(2022) determined that based on genotypic tolerance, the tomato genotype RIOGRANDI presented higher heavy metal tolerance due to wastewater irrigation and differed in patterns of gene action and their inheritance among the studied genotypes. Furthermore, Khan et al. (2023) detected that WRKY and bHLH were essential factors in cadmium stress tolerance of tomato, which provided a fresh insight into the development of new heavy metal stress-tolerant varieties.

3.5 GENETIC COMPONENTS AND DERIVED PARAMETERS

Data were subjected to half diallel analysis according to Hayman (1954b) with the purpose of determining

Table 3a: Components of genetic variances and their derived parameters for fruit yield and yield-related traits under non-Cd stressed (NCS) and Cd stressed conditions (CS)

		Plant height	Branches plant ⁻¹	Fruit set	Fruit mass
D	NCS	11.60 ± 4.19**	0.41 ± 0.17*	20.82 ± 17.61	59.32 ± 9.95**
	CS	4.47 ± 4.45	0.47 ± 0.22*	44.15 ± 16.25**	7.78 ± 10.84
F	NCS	4.15 ± 10.23	0.08 ± 0.41	30.34 ± 43.02	48.25 ± 24.30*
	CS	2.80 ± 10.87	0.15 ± 0.53	70.15 ± 39.70	6.23 ± 26.49
H ₁	NCS	58.78 ± 10.63**	2.24 ± 0.42**	523.60 ± 44.71**	284.89 ± 25.26**
	CS	50.71 ± 11.29**	1.90 ± 0.55**	302.89 ± 41.26**	180.59 ± 27.52**
H ₂	NCS	54.60 ± 9.50**	1.53 ± 0.38**	379.99 ± 39.94**	212.51 ± 22.56**
	CS	44.97 ± 10.09**	1.85 ± 0.49**	254.97 ± 36.86**	158.09 ± 24.59**
h ²	NCS	148.45 ± 6.39**	2.27 ± 0.25**	807.05 ± 26.88**	508.57 ± 15.19**
	CS	112.22 ± 6.79**	4.80 ± 0.33**	371.26 ± 24.81**	498.05 ± 16.55**
(H ₁ /D) ^{0.5}	NCS	2.25	2.34	5.01	2.19
	CS	3.37	2.00	2.62	4.82
H ₂ /4H ₁	NCS	0.23	0.17	0.18	0.19
	CS	0.22	0.24	0.21	0.22
K _D /K _R	NCS	1.17	1.09	1.34	1.46
	CS	1.21	1.17	1.87	1.18
h ² /H ₂	NCS	2.72	1.48	2.12	2.39
	CS	2.50	2.59	1.46	3.15
h ² (n.s)	NCS	0.26	0.52	0.40	0.42
	CS	0.20	0.21	0.14	0.21
H ² (b.s)	NCS	0.88	0.90	0.97	0.95
	CS	0.79	0.73	0.98	0.88

Where: NCS = Non-Cd stressed; CS = Cd stressed; D = additive genetic variance; F = mean of the covariance between additive and dominance effects; H₁ = dominance variance; H₂ = proportion of dominance variance attributable to unequal frequencies of alleles; h² = dominance component of genetic variance; (H₁/D)^{0.5} = average degree of dominance; H₂/4H₁ = proportion of genes with positive and negative effects in the parents; KD/KR = ratio of dominant to recessive alleles in the parents; h²/H₂ = number of gene groups controlling the trait; h² (n.s) = narrow-sense heritability; H² (b.s) = broad-sense heritability. * and ** indicate significance at the 5 % and 1 % probability levels, respectively.

the components of genetic variance and their ratios for all the studied traits. Therefore, the results are presented in Table 3 to better understand the genetic variability in the studied traits under both experimental conditions.

The additive genetic component 'D' was positive under both Cd-free and Cd-stressed conditions for all the studied traits, achieving highly significant or significant at $p \leq 0.01$ or $p \leq 0.05$ probability level, respectively, with a few exceptions of fruit set in Cd-free stressed conditions and branches and fruit set in Cd-stressed conditions. This showed that all the traits studied were heritable, having a positive additive genetic basis that can be inherited from generation to generation. These traits add to their manifestation, and the process was further enhanced by selection to achieve new variety development. In this regard, Godinho *et al.* (2024) reported that the traits measured on the tomato plant with high cadmium concentration had low additive genetic variance.

Additionally, significant or highly significant values of dominance have been registered for all the studied features under both conditions, which designated a high presence of dominant alleles in the gene pool of populations. The results of this study showed that the magnitude of dominance for all the traits was higher or significantly higher than additive components; thus, it indicated the presence of dominant alleles in the population's gene pool under both conditions. This, in turn, suggested that the dominance relationship of alleles has played a major role in determining the phenotype. This could be important also for breeding programs and variety development (Rudas *et al.*, 2025). The Genetic explanation of over-dominance helps breeders make informed decisions about which alleles to select that would maximize desirable traits in successive generations. The value of H_1 for all the tomato traits studied was observed to be higher than that of H_2 , indicating that genes are not equally distributed within the parents. This was confirmed by the ratio of $H_2/4H_1$ (< 0.25), which depicted an asymmetrical distribution of genes at loci in parents, thus dominance for the traits under study. It therefore implied that some dominant alleles were more influential in determining the phenotype of the plant than others. Knowing the magnitude of these dominance effects will enable breeders to select for desirable traits with greater efficiency in subsequent breeding programs.

For all the traits studied in the two conditions, the value of F was positive, indicating a larger number of dominant than recessive genes. This was well supported by the high value of K_D/K_R for all the traits. The share of dominant alleles was highly important for expressing these traits in both conditions. A high value of K_D/K_R for all these traits further supported the notion that dominant genes had more impact on the phenotypic variation

observed. Overall, these results put forth the impact of dominant genes in relation to both conditions on the variation of these traits. Overall dominance effects of heterozygous loci (h^2) were positive and significant for all the studied traits in tomato, meaning that the most dominant genes with positive effects were noted. High ratios of dominant to recessive gene effects (K_D/K_R) and positive dominance variance further support the importance of dominant genes in trait expression (Yadav *et al.*, 2017; Singh *et al.*, 2021). These suggest that when the dominant genes were in their heterozygous state, they would have a desirable impact on the expression of the studied traits in tomatoes. This was so because favorable alleles in dominant genes promote desirable characteristics.

Values of h^2/H_2 in most of the traits studied in tomato indicated that these were governed by a polygenic system, which represented both additive and non-additive genetic effects. Such high values implied that the genetic variation in these particular traits was mainly because of the additive effects of alleles at various loci. This information was very important to plant breeding programs to enhance these traits through selective breeding and other genetic manipulation strategies (Ye *et al.*, 2021).

The average degree of dominance over all loci, as estimated by the ratio H_1/D under both conditions, exceeded unity for all the studied traits; hence, it pointed towards the role of over-dominance gene effects in the inheritance of the studied traits. This suggested that heterozygotes had a higher fitness than either homozygotes, leading to increased genetic diversity in the population. These over-dominant gene effects can explain the maintenance of genetic variation within a population as a result of adaptation to changed environmental conditions (Bhandari *et al.*, 2023). Moreover, narrow sense heritability estimates obtained were of medium magnitude for branches (0.52), fruit set (0.40), fruit mass (0.42), and locules (0.39) when not under Cd stress, showing that non-additive gene action, especially dominance, was present within the inheritance patterns of certain plant traits.

These traits are probably controlled by multiple genes acting together; as such, selective breeding that focuses on selecting individual genes may not have been as effective as once thought. Knowledge of the role of dominance in the mode of inheritance of these traits will be important in devising strategies to improve overall crop productivity. However, for the rest of the displayed traits, low narrow sense heritability was recorded under non-Cd stressed or under Cd stressed conditions, showing that dominance gene action rather than additive gene action was the main contributor to their expression (Ene *et al.*, 2023). That suggested that a few major genes with

Table 3b: Components of genetic variances and their derived parameters for fruit yield and yield-related traits under non-Cd stressed (NCS) and Cd stressed conditions (CS)

		Fruit yield Plant ⁻¹	Locules Fruit ⁻¹	Flesh thickness	Total soluble solids
D	NCS	0.16 ± 0.06**	0.41 ± 0.07**	0.30 ± 0.15*	0.31 ± 0.08**
	CS	0.11 ± 0.08	0.18 ± 0.12	0.22 ± 0.17	0.31 ± 0.26
F	NCS	0.06 ± 0.15	0.21 ± 0.16	0.11 ± 0.37	0.20 ± 0.19
	CS	0.06 ± 0.20	0.21 ± 0.30	0.22 ± 0.42	0.43 ± 0.63
H ₁	NCS	1.17 ± 0.16**	1.22 ± 0.17**	1.94 ± 0.38**	2.04 ± 0.20**
	CS	0.82 ± 0.21**	1.50 ± 0.31**	1.31 ± 0.44**	1.66 ± 0.66*
H ₂	NCS	1.04 ± 0.14**	1.07 ± 0.15**	1.85 ± 0.34**	1.90 ± 0.18**
	CS	0.75 ± 0.18**	1.32 ± 0.28**	1.09 ± 0.39**	1.41 ± 0.59*
h ²	NCS	3.28 ± 0.10**	2.11 ± 0.10**	3.84 ± 0.23**	4.04 ± 0.12**
	CS	2.02 ± 0.12**	1.58 ± 0.19**	1.53 ± 0.26**	1.39 ± 0.39**
(H ₁ /D) ^{0.5}	NCS	2.69	1.72	2.53	2.55
	CS	2.68	2.92	2.42	2.30
H ₂ /4H ₁	NCS	0.22	0.22	0.24	0.23
	CS	0.23	0.22	0.21	0.21
K _D /K _R	NCS	1.15	1.35	1.16	1.28
	CS	1.21	1.53	1.51	1.85
h ² /H ₂	NCS	3.14	1.97	2.08	2.12
	CS	2.68	1.20	1.40	0.99
h ² (n.s)	NCS	0.28	0.39	0.23	0.20
	CS	0.22	0.16	0.25	0.14
H ² (b.s)	NCS	0.91	0.97	0.97	0.97
	CS	0.89	0.94	0.86	0.90

Where: NCS = Non-Cd stressed; CS = Cd stressed; D = additive genetic variance; F = mean of the covariance between additive and dominance effects; H₁ = dominance variance; H₂ = proportion of dominance variance attributable to unequal frequencies of alleles; h² = dominance component of genetic variance; (H₁/D)^{0.5} = average degree of dominance; H₂/4H₁ = proportion of genes with positive and negative effects in the parents; K_D/K_R = ratio of dominant to recessive alleles in the parents; h²/H₂ = number of gene groups controlling the trait; h² (n.s) = narrow-sense heritability; H² (b.s) = broad-sense heritability. * and ** indicate significance at the 5 % and 1 % probability levels, respectively.

large effects may control the traits, leading to the low estimates recorded.

4 CONCLUSION

Inheritance of traits under dominance was crucial in developing plants, which could thrive well under stressed environments, hence stressed cadmium conditions. Breeders have the ability to improve the performance and resilience of tomatoes by selecting genotypes with dominant genes for key traits. The knowledge of non-additive gene action and dominance will be essential for future variety development of cadmium-tolerant varieties that survive. Still, it will also show high yield and quality produce. Therefore, in the future development of cadmium tolerance varieties, it will be imperative to have in great

detail the information about the role that dominance plays during the inheritance of traits.

Author contributions

Conceptualization, original draft preparation, editing, and supervision, Khalid M. Al-Rohily and Raed Ammar Alsufyani; original draft preparation, and validation, Abdulrahman Bin Jumah; writing, review and data visualization, Maha M. Alsubaie and Haya R. Alzannan; methodology, Mohamed Ali Abdelsatar; data curation, Burhan Zain Fakhurji, and formal analysis and editing, Mohamed M. Hassona. All authors have read and agreed to the published version of the manuscript.

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The authors declare no competing interests.

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