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HAYMAN'S DIALLEL ANALYSIS FOR PHYSIOLOGICAL TRAITS IN CHILI (*CAPSICUM ANNUUM* L.) SEEDS

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SUMMARY

Genetic parameters' estimation using Hayman's diallel approach commenced in 2023 on chili (*Capsicum annuum* L.) F₁ hybrid populations developed through the Hardy-Weinberg equilibrium. The prevailing study aimed to acquire information about various genetic parameters and gene action that control the chili seeds' viability using Hayman's diallel analysis approach. The results revealed that all observed variables had the additive gene action managing them. The distribution of genes in the parental genotypes for the probed traits was uneven, with all features controlled by 1–2 genes. The heritability values in broad sense (79.05–96.23) and narrow sense (72.99–84.81) were high on most chili traits. The present information is suitable for determining the direction of cultivars for production in subsequent breeding activities. Information about the genetic parameters can benefit a considerable basis in future breeding programs, especially seed viability in chili.

Key words: Additive and dominance effects, genes, genetic parameters, heritability, seed viability

Key findings: The results revealed that an additive gene action controlled all the variables. The broad sense heritability (h^2_{bs}) values were high for all the traits, while the narrow meaning heritability (h^2_{ns}) values were elevated only for some.

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INTRODUCTION

One of the horticultural plants that is imperative in life is the chili plant (Kirii *et al.*, 2017). The demand for chilies increases with

increasing human needs, requiring continuous production, but the increase lowers seed quality. Plant breeding activities can solve these problems by utilizing existing genetic material to produce new, superior varieties

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(Sreenivas *et al.*, 2020). An easy-to-use technique is artificial hybridization (Kalve and Tadege, 2017). Ganefianti *et al.* (2019) stated that hybridization aims to combine the genetics of two parents to produce new varieties by exploiting the phenomenon of heterosis. Information about the genetic parameters is necessary to improve the characteristics of a population. Genetic parameters can support breeders in managing an efficient breeding program because of their vital role in enhancing *Capsicum annum* L. (Ekowahyuni *et al.*, 2015). Several chili studies have shown that traits can benefit selection criteria with those variables closely associated with yield components and certain vegetative features (Syukur *et al.*, 2010; Istiqlal *et al.*, 2014). Less diallel studies about estimating genetic parameters, especially related to seeds' viability in the chili, have continued; therefore, this work has a greater scope for such studies.

Assembling high-yielding chili cultivars with seed viability characteristics is one of the vital methods in plant breeding that can use diallel cross analysis (Sreenivas *et al.*, 2020). In past studies, the diallel analysis succeeded in attaining the mechanisms of the genes involved in the inheritance of various traits in early segregating generations (Bisen *et al.*, 2017). Hayman (1954) reported that diallel analysis could help predict gene interactions, dominant and additive influences, and gene distribution and also determine the heritability values in a broad and narrow sense. Hayman's genetic analysis aims to obtain information on the inheritance of observed attributes (Gami *et al.*, 2020).

Diallel cross analysis with Hayman's approach has widespread use in studying the genetic basis of various traits in chili, including genetic parameters' evaluation in early generations for begomovirus resistance and agronomic features (Ganefianti *et al.*, 2015), host plant resistance in chili pepper (Daryanto *et al.*, 2017), yield and spiciness components (Sahid *et al.*, 2021), bacterial wilt disease resistance in chili (Dhillon *et al.*, 2022), evaluation of secondary metabolites in chili (Syukur *et al.*, 2023), and rice genotypes for yield-related traits (Riyanto *et al.*, 2023).

Hayman's diallel analysis is suitable to estimate several genetic parameters, including gene interaction, additive and dominance influence, distribution of genes within the parents, level of control, F_1 mean deviation from the parental mean, dominance direction, and sequence, the number of genes controlling the specific trait, and traits heritability (broad and narrow sense) (Hayman, 1954). Information about traits' inheritance is valuable for planning and implementing breeding strategies that lead to genetic improvement (Rukundo *et al.*, 2017). Detailed information about the gene action of selected characteristics is essential for running the breeding program efficiently with the appropriate selection of parental genotypes.

The genetic control components also assist the breeders in selecting the desired parental genotypes for hybridization and the method of selection used for choosing the promising populations. Therefore, the practical study aims to attain information about the genetic parameters and gene action involved in controlling the seeds' viability components in chili genotypes and develop an effective chili breeding program.

MATERIALS AND METHODS

The genetic material comprised six chili (*Capsicum annum* L.) parental genotypes and 30 F_1 cross combinations developed through complete diallel crosses. The crossing program started in 2022 at the Ciampea Bogor Screen House, West Java, Indonesia, with a location height of 250 masl. Assessing chili F_1 hybrid populations compared with parental genotypes commenced in 2023 at the Department of Agronomy and Horticulture, Faculty of Agriculture, Bogor Agricultural University, Indonesia. The parental genotypes came from the collection at the Plant Breeding Education Laboratory, Bogor Agricultural University, Indonesia, namely, chili genotypes with high germination rates (Ungara and F12.145291), medium germination rates (Triwarsana and F7.110053) and low germination rates (Adelina and Viola). The experiment comprising F_1

hybrid populations and parental genotypes of chili continued in a randomized completely block design (RCBD) with three replications. Each experimental unit had 50 seeds earlier germinated in a plastic box with a CD paper substrate placed in an electric germinator at a constant temperature of 28 °C and humidity of 70%–80%.

Observation of chili viability tests followed the standard procedures of the International Seed Testing Association (ISTA) (2018), including germination, radicle emergence, maximum growth potential, vigor index, and dry weight of healthy sprouts.

- a) Germination (%): The germination percentage calculation consisted of the number of normal seedlings in the first (7th day) and second (14th day) observations based on ISTA (2018) per the equation below:

$$\text{Germination} = \frac{\Sigma(\text{normal seedling first count} + \text{normal seedling final count})}{\Sigma \text{planted seeds}} \times 100\%$$

- b) Maximum growth potential (%): The highest growth potential (%) computation was according to the percentage of all healthy and abnormal sprouts until the end of the observation as per the equation below (Sadjad, 1993):

$$\text{Maximum growth potential} = \frac{\Sigma \text{seeds that grow until the end of the observation}}{\Sigma \text{planted seeds}} \times 100\%$$

- c) Vigor index (%): The vigor index (%) proceeded on the number of normal seedlings on the first count (7th day) of germination per the following equation (Copeland and McDonald, 2001):

$$\text{Vigor index} = \frac{\Sigma(\text{normal seedling first count})}{\Sigma \text{planted seeds}} \times 100\%$$

- d) Dry weight of normal germination (g): Calculating the dry weight of the normal germination (g) included the end of the germination test observation (14th day). Removing all the healthy sprouts from the germination medium entailed

wrapping them in an envelope and then drying them in the oven (80 °C for 24 h). After that, the sprouts were placed in a desiccator for ± 30 min before weighing.

- e) Radicle emergence (%): The counting of seeds ensued with roots appearing ≥ 2 mm, as required by the ISTA (2018). The observations continued every 24 h for 168 h (Kusumawardana *et al.*, 2019). The radicle emergence test calculation followed the formula:

$$\text{Radicle emergence} = \frac{\Sigma \text{emergence radicle} > 2 \text{ mm}}{\Sigma \text{germinated seeds}} \times 100\%$$

Estimating genetic parameters commenced using the Hayman approach (Singh and Chaudhary, 1979; Kumar *et al.*, 2018). All the data analysis first went through ANOVA and later through Hayman analysis. ANOVA ran according to the generalized linear model (GLM) using the SAS software package 9.0. Genetic analysis using the Hayman approach transpired on the viability components of chili seeds. The various genetic parameters recorded included gene interactions, additive and dominant influences, distribution of genes in parental genotypes, level of dominance, direction and order of control, number of gene groups controlling the characteristics, and heritability (broad and narrow sense) values.

RESULTS

According to the analysis of variance, the chili F_1 populations and their parental genotypes showed significant ($P \leq 0.01$) differences for the traits, viz., germination, radicle emergence, healthy seedling dry weight, maximum growth potential, and vigor index (Table 1). It revealed that the studied chili F_1 populations and their parental genotypes have a broader genetic variability and scope for further improvement for such traits. Past studies also reported significant differences in F_1 populations and their parental genotypes for various growth-related traits (Salam *et al.*,

Table 1. Analysis of variance in chili genotypes for various traits.

Source of variation	d.f.	Mean squares				
		Germination	Radicle emergence	Dry weight of healthy sprouts	Maximum growth potential	Vigor index
Replications	2	128.6461	128.9259	0.0002	206.3333	182.2593
Genotypes	35	2823.9149**	2878.9037**	0.0021**	3322.2381**	916.5069**
Error	70	175.9604	181.4212	0.0002	92.4667	123.4783
CV (%)		23.13	25.66	31.64	15.01	64.45

Note: ** significant at a level of 1%; CV: Coefficient of variation; d.f. = degree of freedom.

Table 2. Estimation of genetic parameters of chili seed viability components.

Genetic parameters	Chili characters					
	Germination	Radicle emergence	Dry weight of healthy sprouts ^T	Maximum growth potential	Vigor index	
b (Wr, Vr)	0.70 ^{NS}	0.84 ^{NS}	0.8809 ^{NS}	0.83 ^{NS}	0.6974 ^{NS}	
D	1465.16**	1295.69**	0.7502**	1581.75**	279.8519**	
F	392.87 ^{NS}	216.63 ^{NS}	0.1968*	276.05 ^{NS}	-71.9901 ^{NS}	
H ₁	616.23**	490.49**	0.2663**	512.87*	59.0370 ^{NS}	
H ₂	448.52*	373.06*	0.1885**	385.73*	48.2683 ^{NS}	
h ²	680.09**	483.81**	0.3280**	151.29 ^{NS}	10.6433 ^{NS}	
E	58.22 ^{NS}	59.99*	0.0436**	31.88 ^{NS}	41.7037**	
(H ₁ /D) ^{1/2}	0.65	0.62	0.5958	0.57	0.4593	
H ₂ /4H ₁	0.18	0.19	0.1770	0.19	0.2044	
Kd/Kr	1.52	1.31	1.5646	1.36	1.0000	
h ² /H ₂	1.52	1.30	1.7399	0.39	0.2205	
h ² ns	78.45	79.61	78.30	84.81	72.9905	
h ² bs	92.63	92.02	87.81	96.23	79.05	
(h ² _{ns} / h ² _{bs})	0.85	0.87	0.89	0.88	0.92	

Note: b(Wr, Vr) = Covariance-variance regression, D = Additive effect, F = Fr mean, H₁ = Dominance effect, H₂ = Proportion of dominance due to positive and negative effect of genes, h² = F1 deviation from the average parent, E = Environment, (H₁/D)^{1/2} = Mean degree of dominance, H₂/4H₁ = Proportion of positive genes to negative genes, h²/H₂ = Number of groups of genes, h²bs = Broad-sense heritability, h²ns = Narrow-sense heritability; ** significant at a level of 1%; * significant at a level of 5%; NS: Non-significant; ^T = transformed data is used.

2017; Kumar *et al.*, 2018). Estimating genetic parameters can apply if the population owned significant ($P \leq 0.05/P \leq 0.01$) differences for the observed characters (Singh and Chaudhary, 1979). Genetic parameters' estimation using cross-diallel analysis can continue if the average of the squared results for the genotypes and the mean squared error for the observed characters has a probability below 0.01 (Mudhalvan and Kumar, 2020).

Gene interaction

The predominant role of gene interaction in determining genetic diversity in the genotypes

of *Capsicum annum* L. can be visible from the value of b (Wr [covariance], Vr [variance]). If the t-test significantly differed from one, then there is interaction between genes; however, if the value of b is not substantially different from the unit, no gene interaction exists (Roy, 2000; Istiqlal *et al.*, 2014). The regression coefficient b (Wr, Vr) test showed that all the tested parameters were not significantly different by one, indicating no gene interaction in these studied characteristics (Table 2). Results further confirmed that no trait manifested gene interaction, indicating the fulfillment of one of the assumptions of a diallel cross analysis.

Additive (D) and dominance (H₁) effects

Each observed variable has a significant additive effect (D) and dominance (H₁) component, except for the vigor index trait, where the influence of control was not significant (Table 2). The additive effect (D) value emerged higher than the dominance effect (H₁) (Table 2). The impact of the additive gene action was also better than the dominant gene action for each characteristic. It also authenticates and provides information that the next generation can inherit the attribute, and thus, the conclusion that the additive gene action influences the appearance of all the observed characteristics in *Capsicum annuum* L. (Anandhi and Khader, 2011; Istiqlal *et al.*, 2014).

Distribution of genes within the parents

In diallel analysis, the H₂ value is the presentation of the genes' distribution in each parental genotype of *Capsicum annuum* L. Germination characteristics, radicle emergence, dry weight of healthy seedlings, and maximum growth potential had a non-uniform distribution of genes within the parental cultivars, as confirmed by the significant H₂ value (Table 2). The magnitude of the H₁ value compared with the H₂ value indicates the wider scattering proportion of positive genes among the parental genotypes of chili (*Capsicum annuum* L.) (Yunianti *et al.*, 2011; Istiqlal *et al.*, 2014). The experiment showed that positive genes were more involved than negative genes in determining each observed trait of chili, and the same is also valid by the higher value of H₁ than H₂ value (Table 2). The large number of positive gene influences provides advantages for production characteristics in chilies (Yunianti *et al.*, 2011).

Dominance level

The magnitude of the influence of dominance can be perceivable from the ratio of H₁/D^{1/2}. If the value (H₁/D)^{1/2} is between zero and one, it indicates partial dominance; however, if the value (H₁/D)^{1/2} is higher than one, it indicates overdominance (Hayman, 1954). For all the

studied traits of chili, the rates of (H₁/D)^{1/2} were between zero and one; thus, each character occurred with a partial dominance level (Table 2). Additive gene action affecting each character results in each characteristic's appearance tending to approach the mid-parent value and not be over-dominant, which also exceeds the best parental genotypes of chili.

The number of dominant genes in the chili parental genotypes also reflected a positive F value (Yunianti *et al.*, 2011). The vigor index characteristic has a negative F value (-71.9901), indicating not many dominant genes in the parents. In contrast, the characteristics of germination power, radicle emergence, dry weight of healthy seedlings, and maximum growth potential revealed positive F values (392.87, 216.63, 0.1968, and 276.05, respectively), implying the existence of several dominant genes in the chili (*Capsicum annuum* L.) parental genotypes.

Direction and sequence of dominance

In *Capsicum annuum* L., the ranking of genotypes dominance for germination traits was F12.145291 (431.08), Ungara (683.05), F7.110005 (933.27), Viola (1239.50), Adelina (1265.49), and Triwarsana (2048.55) (Table 3). The position of the parental genotypes closer to point zero indicates that the genotype has the most dominant genes. Conversely, if it was farther from the zero point, the genotype contains the most recessive genes (Novita *et al.*, 2007). The chili parental genotype F12.145291's germination trait had the most dominant genes because it showed closeness to the zero point (Figure 1).

The dominant genotypic sequences for the appearance of radicles were Ungara, F7.110005, Adelina, F12.145291, Viola, and Triwarsana (Table 3). The chili parental genotype Ungara for the radicle appearance contained the most dominant genes because it was closer to the zero point (Figure 2). For the trait dry weight of healthy sprouts, the chili parental genotypes' dominance order was F12.145291, Ungara, F7.110005, Viola, Adelina, and Triwarsana (Table 3). The parental genotype F12.145291 for dry weight

Table 3. Distribution of variance + co-variance (Vr + Wr).

Chili genotypes	Germination	Radicle emergence	Dry weight of healthy sprouts	Maximum growth potential	Vigor index
Adelina	1265.49 (5)	908.85 (3)	0.0009 (5)	1167.29 (4)	327.51 (4)
Triwarsana	2048.55 (6)	1823.72 (6)	0.0011 (6)	2245.68 (6)	502.47 (6)
Ungara	683.05 (2)	493.20 (1)	0.0005 (2)	671.01 (1)	132.40 (1)
Viola	1239.50 (4)	1054.21 (5)	0.0007 (4)	1360.68 (5)	215.82 (5)
F12.145291	431.08 (1)	1028.66 (4)	0.0004 (1)	755.90 (2)	220.09 (2)
F7.110005	933.27 (3)	877.74 (2)	0.0005 (3)	1001.94 (3)	353.24 (3)

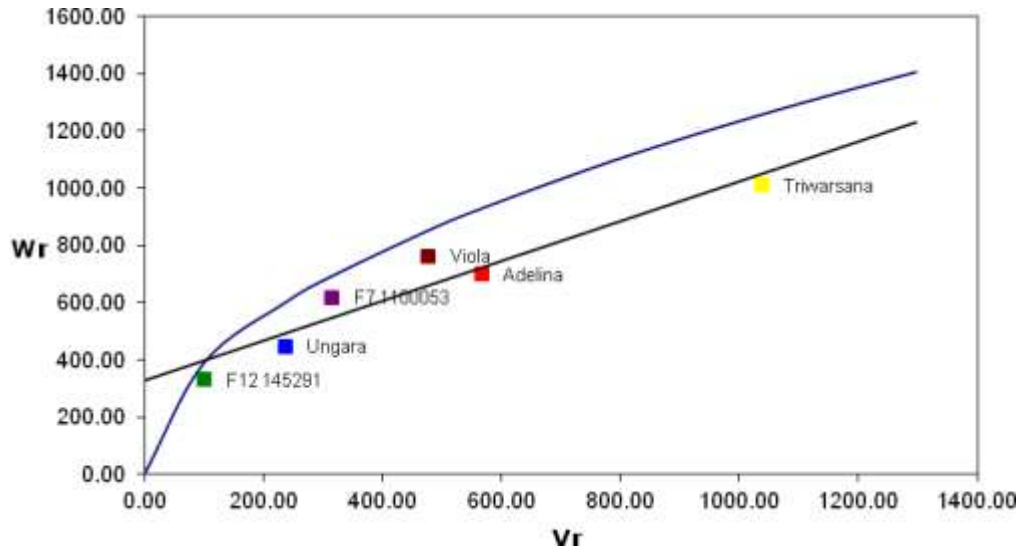


Figure 1. Relationship of covariance (Wr) and variance (Vr) for germination percentage in chili.

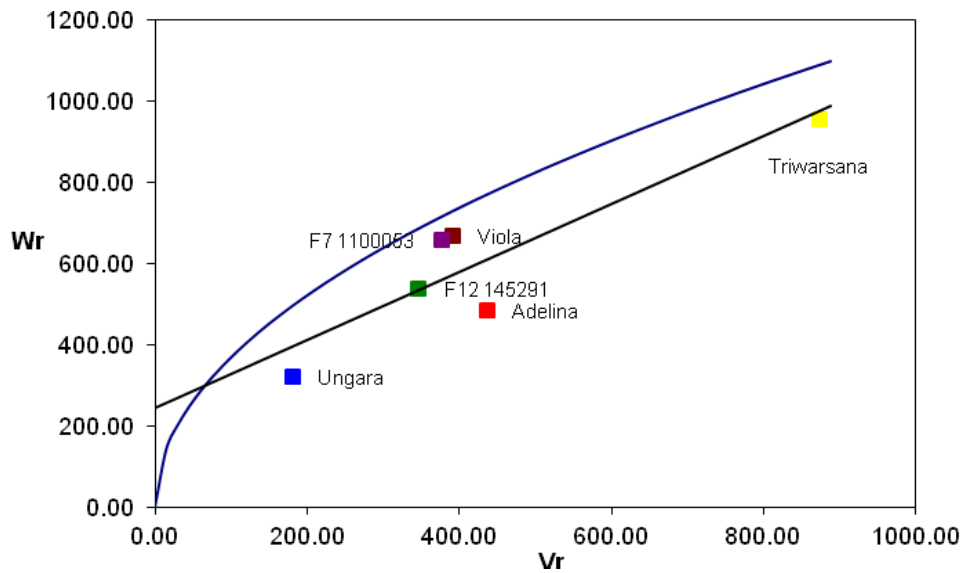


Figure 2. Relationship of covariance (Wr) and variance (Vr) for radicle emergence in chili.

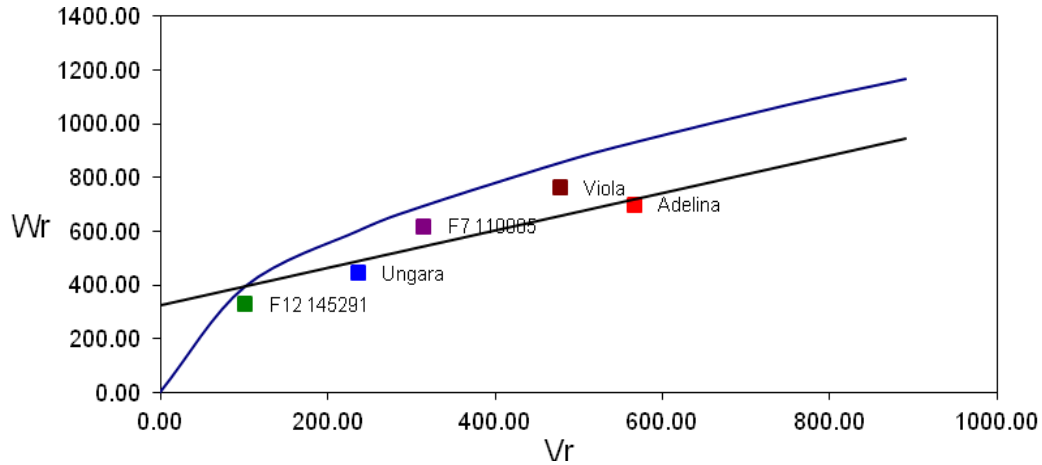


Figure 3. Relationship of covariance (Wr) and variance (Vr) for dry weight of healthy sprout in chili.

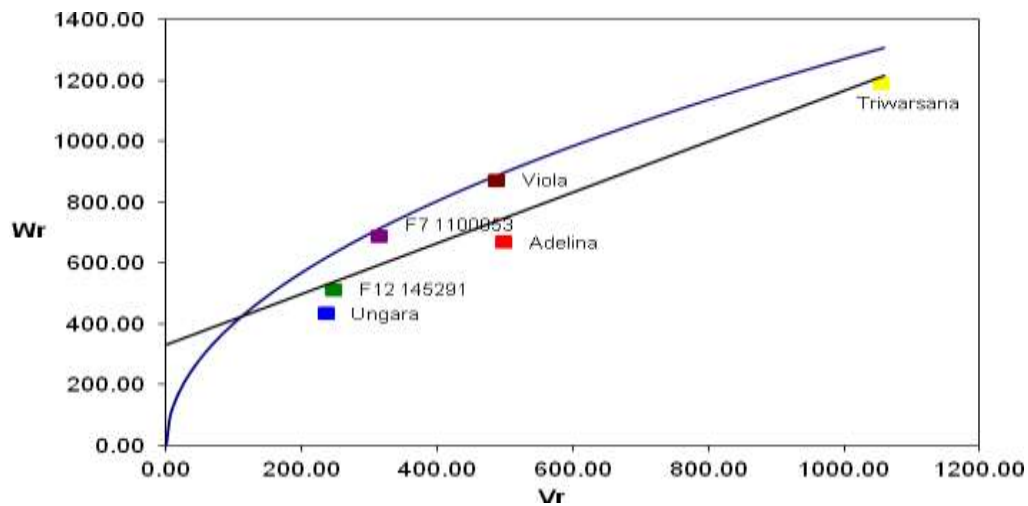


Figure 4. Relationship of covariance (Wr) and variance (Vr) for maximum growth potential in chili.

of robust sprouts had the most dominant genes due to their closeness to the zero point (Figure 3).

For the trait maximum growth potential, the dominance sequences of the chili parental genotypes were Ungara, F12.145291, F7.110005, Adelina, Viola, and Triwarsana (Table 3). The chili parental genotype Ungara contains the most dominant genes for such a feature because it was closest to the zero point (Figure 4). The trait vigor index has the same order of dominance in the chili parental genotypes with the maximum growth potential, i.e., Ungara, F12.145291, F7.110005, Adelina,

Viola, and Triwarsana (Table 3). The chili (*Capsicum annum* L.) parental genotype Ungara’s vigor index contains the maximum dominant genes with the closest proximity to the zero point (Figure 5).

Gene groups controlling parameters

The ratio of h^2/H_2 indicates the number of gene groups that control a trait in plants. The chili (*Capsicum annum* L.) variables, i.e., maximum growth potential and the vigor index in this experiment, had h^2/H_2 values of 0.39 and 0.2205, respectively, which authenticated

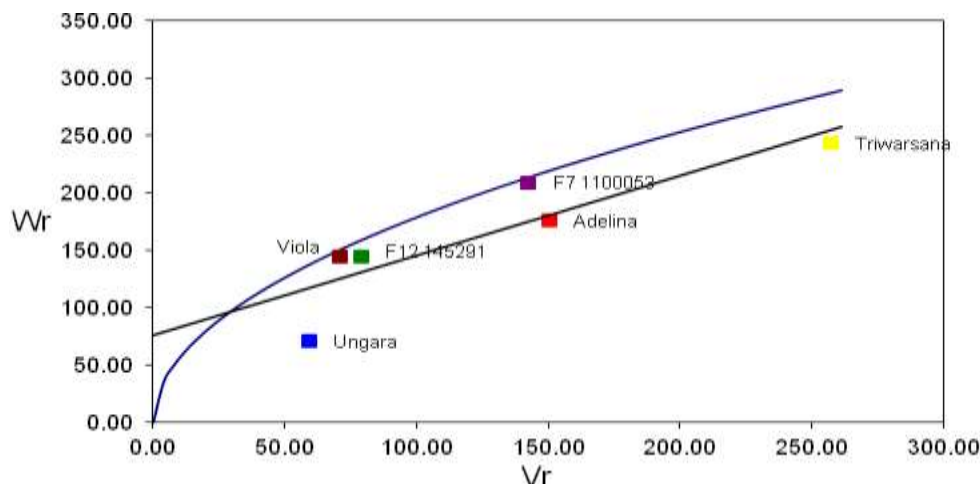


Figure 5. Relationship of covariance (W_r) and variance (V_r) for seed vigor index in chili.

that one gene group controlled these two features. However, the chili's other three parameters, viz., germination percentage, radicle emergence, and dry weight of healthy sprouts, had h^2/H_2 ratios of 1.52, 1.30, and 1.7399, respectively (Table 2), indicating that these three characteristics had two groups of genes controlling them.

Heritability

The broad sense heritability (h^2_{bs}) estimates were the highest for chili (*Capsicum annuum* L.) traits, i.e., germination rate (92.63%), radicle emergence (92.02%), dry weight of healthy sprouts (87.81%), maximum growth potential (96.23%), and vigor index (79.05%) (Table 2). These heritability values authenticated that the observed chili characteristics were mainly controlled by genetic factors and less by environmental conditions (Geleta and Labuschagne, 2006).

The narrow sense heritability (h^2_{ns}) estimates for all the chili attributes also incur a high category, namely, germination rate (78.45%), radicle emergence (79.61%), dry weight of healthy sprouts (78.30%), maximum growth potential (84.81%), and vigor index (72.99%) (Table 2). These narrow sense heritability values indicate that the proportions of observed additive variances were high for most of the chili characteristics.

The average ratios of heritability in the broad and narrow sense for chili traits were 0.85 for germination rate, 0.87 for radicle emergence, 0.89 for dry weight of healthy sprout, 0.88 for maximum growth potential, and 0.92 for vigor index (Table 2). It revealed that the additive gene action determines the traits, i.e., germination power percentage, radicle emergence, maximum growth potential, vigor index, and the weight of sprouts, compared with the non-additive gene action. The chili traits with additive variances and high heritability in F_1 populations may be further options using an individual plant selection. Single plant selection can apply to parameters with an additive variance and a high heritability in the F_1 populations (Riyanto *et al.*, 2023).

DISCUSSION

The chili (*Capsicum annuum* L.) characteristics of germination percentage, radicle emergence, the dry weight of healthy seedlings, maximum growth potential, and vigor index sustained control by additive gene effects than non-additive. Features controlled by additive role continue to transfer from generation to generation; thus, the improvement will be effective in the next generation by collecting homozygous loci (Syukur *et al.*, 2010; Ganefianti *et al.*, 2018). The knowledge of

dominant and recessive genes has its basis in $W_r + V_r$, and these diagrams aim to know which character has dominant or recessive alleles' control.

Based on Figures 1–5, it can be evident that the genes controlling the chili characteristics were more recessive ones; hence, one can conclude that the traits, i.e., percentage of germination, radicle emergence, the maximum growth potential, dry weight of healthy seedlings, and vigor index sustained management by recessive genes (homozygous loci) in an individual plant. Attributes controlled by recessive genes are more effectively available in the second generation through selfing. It indicates that the selection in chili populations will be effective in the second generation (F_2) (Hapshoh *et al.*, 2016; Sahid *et al.*, 2020).

The order of the dominance showed that more content of the dominant genes was apparent in the chili parental genotypes. The order of dominance of the seed viability traits appears in Table 3. The smaller the value of $W_r + V_r$, the more it contains dominant genes that control a characteristic. In addition, the order of dominance also bore reflection in the image of the relationship of covariance (W_r) and variance (V_r); the closer the parental to the zero, the parent contains the most dominant genes. Conversely, the farther the parent from the zero, the chili (*Capsicum annuum* L.) parental genotypes have the more recessive genes (Singh and Chaudhary, 1979; Istiqlal *et al.*, 2014; Baseerat *et al.*, 2019).

The magnitude of the influence of domination occurred by the ratio $(H_1/D)^{1/2}$. The results showed that the chili traits, i.e., germination %, radicle emergence, dry weight of healthy seedlings, maximum growth potential, and vigor index, were more predominantly managed by dominant genes. It could be due to the uneven distribution of genes in the chili parental genotypes. The values of genes' distribution can be evident from the ratio of $H_2/4H_1$, which was less than 0.25, indicating an uneven distribution of positive and negative genes (Yunianti *et al.*, 2011; Istiqlal *et al.*, 2014).

The results showed an uneven distribution of genes emerged for all the

observed characteristics of chili. Reports of similar results also came from past studies, which showed an uneven distribution of genes in the yield component traits of chili (Fortunato *et al.*, 2015; Pessoa *et al.*, 2019), tomatoes (Saleem *et al.*, 2013; Saputra *et al.*, 2014; Pujer and Badiger, 2017), and radish (Tian *et al.*, 2017). The number of genes that control a trait has the ratio of h^2/H_2 determining it. Results indicated that almost all the observed characters had two genes controlling them, except the traits' maximum growth potential and seed vigor index controlled by one gene.

The heritability (broad and narrow sense) values for most features were high, implying that the observed traits bore control more by genetic than environmental factors (Riyanto *et al.*, 2023). Previous research on chili also showed that the broad sense heritability values were high for yield traits (Istiqlal *et al.*, 2014) and resistance to bacterial wilt (Dhillon *et al.*, 2022). Syukur *et al.* (2010) findings revealed that the heritability predictive values were high for the pepper (*Capsicum annuum* L.) qualities, viz., fruit weight, length, and diameter, and such population applies the direct selection. According to Fehr (1987), if the heritability value is high, then selection can be suitable in the early generations because the inheritance of characteristics of the genotypes by the next generations is easier and more effective. The ratios of heritability in a broad and narrow sense reflect the additive and non-additive roles of gene action for the concerned traits.

CONCLUSIONS

Results revealed that all observed characters had the additive gene action controlling them. The distribution of genes in the chili (*Capsicum annuum* L.) parental genotypes for the observed characters was uneven, with all characters controlled by 1–2 genes. The ratios of heritability in a broad and narrow sense were high for most traits. This information about the genetic parameters will be beneficial in determining the direction of chili cultivars' production in subsequent breeding programs.

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