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INHERITANCE PATTERN AND GENE ACTION OF BIOCHEMICAL ATTRIBUTES IN RAPESEED (*BRASSICA NAPUS* L.)

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Abstract

The knowledge of gene action and inheritance pattern is of prime importance for a breeder to choose the correct breeding strategy for crop improvement. To understand the inheritance pattern of the quality trait in rapeseed, an experiment of 8 × 8 complete diallel crosses was conducted. The scaling test analysis proved the full adequacy of Hayman's additive–dominance model for all traits except oleic acid and erucic acid contents. The analysis showed the role of both additive and dominance gene action in the manifestation of studied traits. The larger values of dominance (H_1, H_2) than additive genetic components of variation (D) indicated the prime importance of the non-additive genetic effect. The E component was also significant specifying unstable expression of these traits due to the environmental influence. The Vr/Wr graph and the average degree of dominance revealed over dominance type of gene action for the studied traits. The scattering of genotypes on the regression line proved sufficient genetic diversity for studied traits among parental genotypes. The distribution of array points revealed that genotypes AUP-05 possessed the most dominant genes whereas genotypes AUP-06 possessed the most recessive genes for most of the studied traits. Heritability analysis also revealed the greater role of dominant genes and environment effect in controlling these traits. From these results, it could be suggested that selection could be effective in later segregating generations for improving these quality parameters.

Key words: Gene actions, Diallel crosses, Genetic components of variance, Heritability, Rapeseed.

Introduction

Rapeseed (*Brassica napus* L.) is an important oilseed crop for the entire world after soybean. The seeds provide high-quality edible oil and a protein-rich meal for feed production. In terms of nutritional value, oilseed rape meal has a well-balanced content of important amino acids (Widiarsih *et al*., 2021). It contains a monounsaturated fatty acid; oleic acid which enhances cooking quality and improves the shelf life of oil during storage (Debonte *et al*., 2012). Linolenic acid is another important fatty acid essential for human health. The human body needs linolenic acid, but cannot be manufactured and must be obtained through diet. One of the key reasons for the increased incidence of cancer, the trend of low age in human sub-health and chronic diseases is the insufficient intake of linolenic acid (Li *et al*., 2019).

Brassica species oil contains a toxic component called erucic acid, which causes fat deposits in the heart and skeletal muscles and also impedes growth (Sauer & Kramer, 1983). As a result, rapeseed oil with a lower level of erucic acid is preferable. Rapeseed meal is high in protein and glucosinolates, a sulfur-containing substance found primarily in green tissue and seeds. Consumption of rapeseed meals in human and animal diets is hampered by the presence of glucosinolates and their hydrolyzed derivatives. However, on the other hand, a sufficient level of erucic acid and glucosinolate in rapeseed is highly suitable for industrial purposes as well as for biofuel production (Ahmad *et al.*, 2012). Because of the negative consequences, breeders are concentrating their efforts to develop promising rapeseed genotypes for edible purposes with lower levels of erucic acid and glucosinolates (Rameeh *et al.*, 2003).

The development of a superior cultivar can be achieved by combining desirable genes from diverse parents through the process of hybridization. However, it is essential to have information regarding the type and magnitude of gene action responsible for the expression of important traits. Gene action knowledge aids in the choice of parents for hybridization projects. It also guides plant breeders to choose an appropriate breeding procedure for the genetic improvement of a particular trait. Gene action in crop plants has been studied with the help of various biometrical techniques such as diallel, partial diallel, triallel, quadriallel, line x tester, generation mean analysis, biparental cross and triple test cross analysis (Khan *et al.*, 2005)

Plant breeders frequently perform diallel analysis to determine the genetic basis of variation in a variety of characteristics (Meena *et al*., 2017). It is useful to determine a population's additive and dominant effects, which can subsequently be used to evaluate genetic variability and heritability. The genetic improvement of rapeseed depends on the nature and magnitude of genetic variability and interactions involved in the inheritance of important traits. In addition, diallel mating generally results in the production of new genetic combinations with better performance than their respective parents (Zhang & Kang, 1997). Keeping in view the above facts the current study was designed to investigate gene action and heritability for oil quality attributes using the Hayman approach to find generation where selection will be important for enhancing these features.

Materials and Methods

To study gene action and heritability, in year-I eight diverse advanced rapeseed lines (AUP-01, AUP-05, AUP-07, AUP-08, AUP-10, AUP-13, AUP-18, and AUP-21) were collected from National Uniform Yield Trial (NUYT) and crossed in complete diallel fashion at The University of Agriculture-Peshawar Pakistan. In year II, the produced 56 F_1 hybrids along with parental lines were evaluated in (Randomized Complete Blocked Design (RCBD) with 3 replications.

Data collection: Data were recorded on oil, protein, oleic acid, linolenic acid, glucosinolate, and erucic acid contents by scanning a sample of 3g from each genotype through Near Infra-red Reflectance Spectroscopy (NIRS) at Nuclear Institute for Food and Agriculture (NIFA) Peshawar-Pakistan.

Biometrical analysis: The data were analyzed for variances according to Steel and Torrie, 1980 method to test the null hypothesis of means equality. The significant data on all parameters were subjected to the Additive-dominance model of Hayman, 1954 to study the genetic basis of variation in the F_1 generation. In this method total sum of squares is divided into components such as "a" (additive), "b" (dominance) "c" (maternal), and "d" (reciprocal). The graphical analysis approach employing Vr/Wr is effective when the relevance of the non-additive component is determined.

Diallel analysis assumptions and tests of adequacy: The validity of information from a set of genotypes attained from diallel method is based on a few assumptions like (a) lack of reciprocal effects (b) homozygosity of parents (c) diploid segregation of chromosomes (d) absence of epistasis (e) lack of multiple allelism and (f) independent dissemination of genes among the parents. For fulfilling assumptions, the data were tested through two scaling tests regression analysis and t^2 test to see the adequacy of the additive-dominance model. According to Mather and Jinks (1982), the regression coefficient is expected to be significantly different from zero and not from unity. Failure of this test means the presence of epistasis. If a certain type of non-allelic interaction is present, the Wr+Vr and Wr-Vr change from array to array. Non-significant value of the t^2 test also indorses the occurrence of no interaction and the genes are independent of the random association. The additive-dominance hypothesis is fully invalidated if these tests fail. Even if the assumptions are met, the additive-dominance model is only considered partially appropriate.

Genetic parameters: The genetic components of variance D (Additive genetic variance), H (Dominance variance), F (dominant to recessive alleles frequency in parents), h^2 (confirms dominance direction), E (Expected environmental effect), $\sqrt{H_1}/D$ (denotes an average degree of dominance), $H_2/4H_1$ (represents the fraction of genes with negative and positive effects in the parents), $\sqrt{4DH_1}+F/\sqrt{4DH_1}-F$ (denotes the ratio of dominant and recessive genes in the parents), h^2/H_2 (denotes the number of gene groups/genes, which control the character and exhibit dominance) were computed.

Estimation of heritability: Broad sense heritability and narrow sense heritability in the F_1 generation were calculated for each character according to the method proposed by Mather & Jinks (1982).

Results and Discussion

The combined analysis of variance (ANOVA) results showed significant mean squares ($p \leq 0.01$) for all studied traits (Table 1), allowing the use of Hayman's (1954) and Jinks (1954) simple additive-dominance model for further analyzing the data. The adequacy of this model was determined through a scaling test of each trait (Table 2). The detailed gene action and inheritance pattern were explored.

Table 1. Mean squares of seed quality traits in 8 × 8 F_1 diallel crosses of rapeseed.

Trait	Mean squares			
	Genotype (df=63)	Replication (df=2)	Error (df=126)	CV (%)
Oil content	236.29**	3.589	2.849	3.943
Protein content	19.25**	0.108	2.632	6.989
Oleic acid content	92.43**	4.198	11.517	6.707
Linolenic acid content	3.88**	0.189	0.378	7.343
Glucosinolate content	435.01**	20.722	16.631	5.229
Erucic acid content	121.93**	0.456	6.138	7.431

** Significant at $p \leq 0.01$ df = Degree of freedom, CV = Coefficient of variance

Table 2. Adequacy tests of additive-dominance model for 8 × 8 diallel in rapeseed.

Traits	t^2 analysis	Regression analysis		
		b=0	b=1	Remarks
Oil content	NS	*	NS	Model was fully adequate
Protein content	NS	NS	*	Model was partially adequate
Oleic acid content	NS	NS	NS	Model was partially adequate
Linolenic acid content	NS	*	NS	Model was fully adequate
Glucosinolate content	NS	**	NS	Model was fully adequate
Erucic acid content	NS	NS	NS	Model was partially adequate

*= Significant at 5 % level of probability level ** = Significant at 1% level of probability level NS = Non significant

Table 3. Mean squares for quality traits in 8 × 8 F_1 diallel cross of rapeseed using Hayman's analysis.

Traits	Mean squares for Hayman analysis							
	a (df = 7)	b (df = 28)	b_1 (df = 1)	b_2 (df = 7)	b_3 (df = 20)	c (df = 7)	d (df = 21)	Error (df =63)
Oil content	362.14**	241.11**	63.01**	278.08**	237.08**	23.51**	79.27**	2.36
Protein content	36.40**	27.48**	55.86**	21.88**	28.03**	2.99ns	5.31**	1.80
Oleic acid content	222.94**	98.26**	132.50**	59.01**	110.28**	17.78ns	41.98**	12.99
Linolenic acid content	14.62**	4.61**	5.00**	3.90**	4.83**	4.14**	1.41**	0.63
Glucosinolate content	752.25**	379.55**	117.86**	762.15**	258..73**	122.15**	113.20**	14.40
Erucic acid content	272.06**	119.00**	109.00**	43.70**	145.81**	20.08**	34.50**	5.25

a = Additive gene effect, b = Dominance gene effect, b_1= Directional dominance deviation, b_2 = Gene distribution among the parents, b_3 = Specific gene effects, c = Maternal effect, d = Reciprocal effect*, ** Significant at $p \leq 0.05$ and $p \leq 0.01$, ns = Non-significant

Table 4. Genetic components of variance for quality traits in F_1 generation of rapeseed.

Genetic components of variance	Value ± standard error					
	Oil content	Protein content	Oleic acid content	Linolenic acid content	Glucosinolate content	Erucic acid content
D	145.627±8.471*	6.788±1.582*	35.923±9.933*	0.618±0.411	371.453±31.616*	52.463±7.426*
H_1	228.101±9.585*	22.141±2.591*	68.350±12.670*	3.264±0.787*	430.371±34.441*	85.441±7.854*
H_2	159.193±6.011*	17.140±1.852*	56.980±9.318*	2.510±0.540*	243.584±18.479*	75.884±6.426*
F	184.57±12.346	8.925±2.467*	29.933±13.608*	0.233±0.653	469.902±46.854*	39.841±9.221*
h^2	8.866±3.578*	7.900±2.977*	17.547±11.449	0.612±0.619	15.219±12.313*	15.281±7.158*
E	0.785±0.098*	0.600±0.077*	4.330±0.530*	2.298±0.739*	4.800±0.579*	1.751±0.226*
$(H_1/D)^{1/2}$	1.252	1.806	1.379	2.298	1.076	1.276
$H_2/4H_1$	0.174	0.193	0.208	0.173	0.141	0.222
KD / (KD + Kr)	0.753	0.682	0.651	0.541	0.810	0.648
Heritability (bs)	0.986	0.905	0.841	0.808	0.950	0.945
Heritability (ns)	0.270	0.227	0.318	0.384	0.318	0.349

In F_1 parameter value is significant when it exceeds 1.96 after dividing it by its standard error. D = Additive variance, H_1 = Dominance variance, H_2 = Dominance variance, F = Dominance to recessive alleles frequency in parents, h^2 = Overall dominance effect due to heterozygosity, E = Environmental effect, $(H_1/D)^{1/2}$ = Average degree of dominance, $H_2/4H_1$ = Proportion of genes with positive and negative effects, KD / (KD + Kr) = Proportion of dominant genes in parents

Adequacy of additive dominance model: The two scaling tests t^2 test and regression analysis for genetic study in F_1 generation showed full adequacy of the model for oil content, linolenic acid content, and glucosinolate content (Table 2). Similarly for protein, oleic acid, and erucic acid content results revealed partial adequacy of the model. The previous rapeseed study also revealed the full adequacy of the additive-dominance models for biochemical characteristics. (Rameeh, 2013 and Ali *et al*., 2014). Moreover, partial adequacy of the additive-dominance model has been reported in *Brassica napus* L. and Indian mustard for these parameters (Qurban *et al*., 2010; Farshadfar *et al*., 2011; Saeed *et al*., 2013 and Bhakal *et al*., 2017).

Mean squares for quality traits using hayman's analysis: In this set of rapeseed genotypes, Hayman's analysis revealed highly significant variances for both the 'a' and 'b' components, indicating the prevalence of both additive and dominant genetic effects for all the variables tested (Table 3). Similarly, the role of additive and dominant genetic effects in the expression of oil and other quality characteristics has been observed in rapeseed; *Brassica napus* L. (Iqbal *et al*., 2003 and Ahmad *et al*., 2015) in turnip rape; *Brassica campestris* L. (Rehman *et al*., 2011), and in Indian mustard; *Brassica juncea* L. (Shweta *et al*., 2007). The higher proportion of 'a' than 'b' components for all studied traits indicated the more prevalence of additive genetic effect among parents as previously observed in rapeseed (Variath *et al*., 2009 and Ahmad *et al*., 2015). However, the importance of non-additive gene action has been reported for oleic acid in turnip rape and for oil content in Indian mustard (Nasim & Farhatullah, 2013 and Mohan *et al*., 2017). Dominance components; 'b_1', 'b_2' and 'b_3' were highly significant for the studied attributes showing directional dominance deviation of genes, asymmetrical genes distribution among the parents and specific genes effect, respectively. The 'b_2' component of dominance was greater than 'b_3' and 'b_1', showing directional dominance deviation of genes in the expression of oil content and glucosinolate content. For erucic acid content, the 'b_3' component was greater showing the expression of specific genes for this trait among parents. While for protein, oleic and linolenic acid contents 'b_1' value is greater indicating directional dominance deviation of genes in these traits expression. The 'c' and 'd' components were highly significant except for protein content and oleic acid content showing the importance of maternal and reciprocal effect among parents for studied traits (Table 3). Similarly, results were earlier reported in rapeseed for the expression of oil content and linolenic acid content (Zhang *et al*., 2004 and Wang *et al*., 2010).

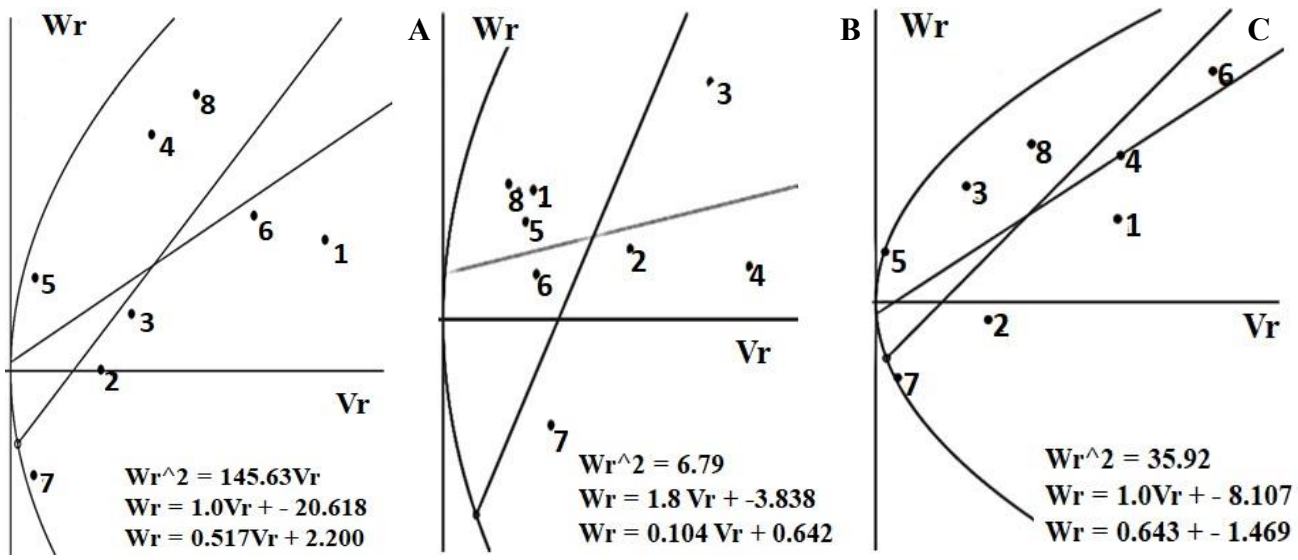

Fig. 1. Vr/ Wr graph for a) oil content, b) protein content and c) oleic acid content in F_1 generation of rapeseed.
Genotypes 1 = AUP-1, 2 = AUP-5, 3 = AUP-7, 4 = AUP-8, 5 = AUP-10, 6 = AUP-13, 7 = AUP-18, 8 = AUP-21

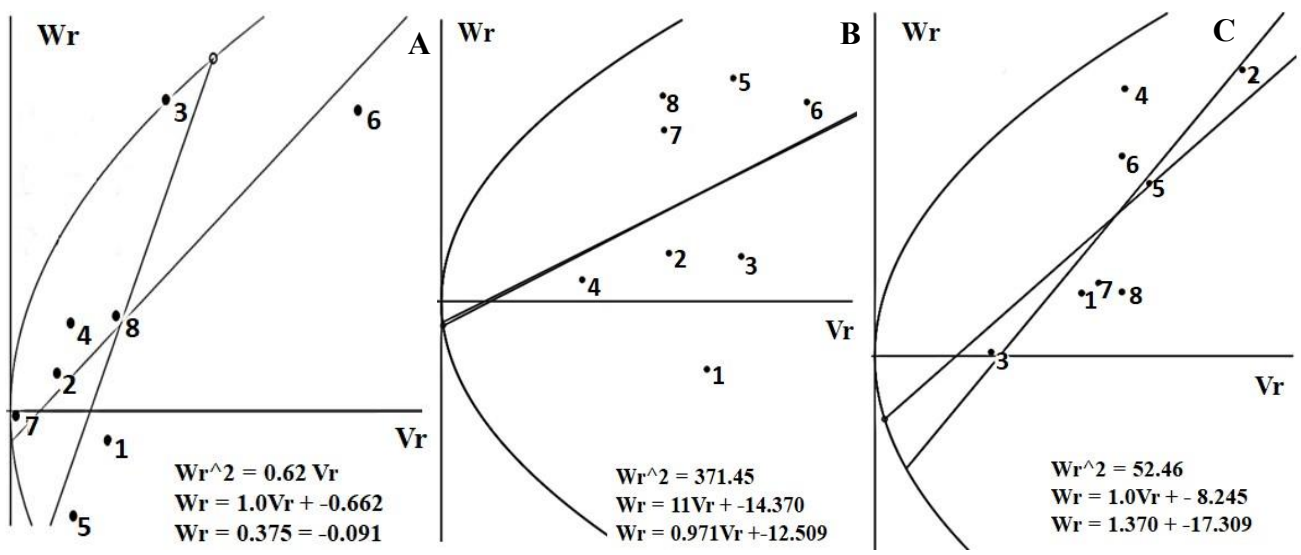

Fig. 2. Vr/ Wr graph for a) linolenic acid content b) glucosinolate content and c) erucic acid content in F1 generation of rapeseed.
Genotypes 1 = AUP-1, 2 = AUP-5, 3 = AUP-7, 4 = AUP-8, 5 = AUP-10, 6 = AUP-13, 7 = AUP-18, 8 = AUP-21

Genetic components of variance in F_1 generation: Estimates of genetic parameters showed the significance of 'D' and 'H' (H_2 and H_1) components indicating the importance of both additive and dominance gene effects in the manifestation of studied parameters in rapeseed genotypes (Table 4). Concomitantly the involvement of both gene actions for quality attributes was also reported earlier in rapeseed and Indian mustard (Thakral *et al*., 2000; Rameeh *et al*., 2003 and Shweta *et al*., 2007). While for linolenic acid the 'D' component was non-significant signifying only the dominance genetic effect for this trait. Similar results were earlier observed in Indian mustard lines (Shrimali *et al*., 2017). The average degree of dominance [$(H_1/D)^{1/2}$; 1.25; being greater than unity], reflects over dominance gene action for all the biochemical traits which is in line with the earlier findings in rapeseed and Indian mustard (Mohan *et al*., 2017 and Shrimali *et al*., 2017). The 'H_1' and 'H_2' components of dominance were unequal in proportion. Similarly, the ratio of $H_2/4H_1$ [0.17; being less than 0.25] also revealed unequal proportions of genes with positive and negative effects for the expression of studied attributes in parents. The 'F' value was positive and significant for all the studied attributes, suggesting the higher frequency of dominant alleles among parental genotypes. The proportion of dominant to recessive genes ratio [KD/ (KD + Kr); 0.75 was positive and greater than 0.5] confirmed the larger fraction of dominant genes in parents. In the same way, Indian mustard findings also revealed a greater proportion of dominant genes than recessive genes (Mohan *et al*., 2017). The 'h^2' (measures overall dominant effect for heterozygous loci) was significant which confirmed that dominance was unidirectional for studied traits. The environmental component 'E' was significant (Table 4) for all traits indicating that due to the influence of the environment these traits were unstable. The results corroborate with earlier findings in Indian mustard (Chandra *et al*., 2018).

Heritability estimates: The analyzed data showed a high (≥60) value for broad-sense heritability while low (≤30) narrow sense heritability presents the principal role of non-additive gene action in governing the studied traits (Table 4). The narrow-sense heritability with low estimates refers to a greater influence of the environment. Breeders mostly rely on this type of heritability and therefore, improving these traits selection will be effective in later segregating generations. Similarly, high broad sense and low narrow-sense heritability were previously estimated in rapeseed experiments (Aytac & Kinaci, 2009; Patel & Vyas, 2011 and Masood *et al*., 2019). However, medium narrow-sense heritability and moderate broad-sense heritability for linolenic acid and glucosinolates content were reported in some Indian mustard lines, rapeseed and *Brassica oleaceae* L. (Zhang & Zhou, 2006; Rameeh, 2011; Shrimali *et al*., 2017 and Chandra *et al*., 2018). While high narrow-sense heritability was reported for quality parameters in rapeseed (Rameeh, 2013).

Vr/Wr graph analysis: The scattering of parental genotypes along the regression line showed considerable genetic variability for oil quality attributes in the studied parental genotypes (Figs. 1, 2). The array points on the regression line showed that parental line AUP-05 being closed to the origin possessed maximum dominant genes for oil, protein, and linoleic acid contents. However, AUP-06 being farther from origin had maximum recessive genes for most of the studied traits. The Vr/Wr graph showed that the regression line intercepted the Vr-axis below the point of origin indicating over dominance gene action for the investigated traits (Figs. 1, 2). Similarly, the intercept of covariance (Wr) by variance (Vr) regression line is negative indicating over dominance gene action which is also confirmed by the greater value of 'H_1' than 'D'. Earlier findings also confirmed over dominance in controlling quality traits in rapeseed and Indian mustard (Iqbal *et al*., 2003; Rai *et al*., 2005; Oghan *et al*., 2009 and Ali *et al*., 2014). Conversely, dominance genetic effects were reported for oil and their quality traits in rapeseed, Indian mustard and turnip rape (Qurban *et al*., 2010; Bhakal *et al*., 2017 and Mumtaz *et al*., 2017).

Conclusions

The analysis showed sufficient genetic variability in the tested material which could exploit in future breeding programs for the improvement of quality traits. Parental genotypes, AUP-05 and AUP-06 possessed more dominant and recessive genes for the desirable and undesirable biochemical traits respectively. Therefore, it is recommended as the best parent and can be implied in future breeding programs for genetic improvement of rapeseed. Environmental factors played a significant role in the expression of the studied trait. From the low narrow-sense heritability and prime role of non-additive gene action, it could be concluded that the selection process will be effective in later segregation generation for the enhancement of desirable quality parameters.

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