

THE GENETIC SYSTEM CONTROLLING AGRONOMIC TRAITS IN CANOLA

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ABSTRACT

To determine the types of combining abilities, heterosis and genetic behavior of agronomic traits, six divergent canola genotypes were crossed using a half diallel mating design (excluding reciprocal crosses). The parents and their crosses were evaluated using a randomized complete block design with three replicates at Kafr-El-Hamam/Sharkia and Etay-El-Baroud/Behaira Agricultural Research Stations, Agricultural Research Center, Egypt. The preponderance of dominance gene action was observed for most studied traits as verified by the average degree of dominance and narrow-sense heritability. The GGE biplot revealed that N.A.36 and N.A.39 at Kafr-El-Hamam and N.A.39 and N.A.14 at Etay-El-Baroud were the best general combiners for seed weight plant¹ and N.A.36, N.A.38 and N.A.39 at Kafr-El-Hamam and N.A.36, N.A.39 and N.A.14 at Etay-El-Baroud for seed oil content, which associated with proportion of desirable genes either dominant or recessive. Superior crosses than better parents for seed weight plant¹ were observed in four crosses [N.A.36 and N.A. 37] x [N.A.38 and N.A.14] at Kafr-El-Hamam and two crosses [N.A.37] x [N.A.38 and N.A.14] at Etay-El-Baroud as well as for seed oil content in four crosses [N.A.39 and N.A.14] x [N.A.37 and N.A.38] at Kafr-El-Hamam and two crosses in [N.A.18] x [N.A.37 and N.A.38] at Etay-El-Baroud.

Key words: *Canola (Brassica napus L.), Gene action, GGE biplot, Graphical analysis, Half diallel analysis.*

INTRODUCTION

Canola (*Brassica napus* L.) was defined with its low contents of erucic acid and glucosinolate, hence it is considered as an important and safe oilseed crop in Egypt. Moreover, its oil is high quality due to its high proportion of unsaturated fatty acids. Thus, it can effectively contribute in narrowing the gap between oil production and consumption requirements. Accordingly, developing genotypes with high yield and quality is one of the biggest challenges for canola breeders. To develop improved genotypes, it is important to determine the genetic behavior of seed yield and its components for identification of suitable parental canola genotypes. A useful tool for this purpose, accordingly, is the diallel analysis using the approach proposed by Jinks (1954) and Hayman (1954 a, b), along with a novel approach proposed by Efe (1995, 1996). In this respect, two types of gene action, either additive or dominance, were estimated in several studies. In the study of Ali *et al* (2015) and Xie *et al* (2018) observed that additive gene action, along with a slight involvement of dominance, predominated in the inheritance of most studied traits. Both additive and non-additive gene actions were important in the expression of investigated traits and preponderance of non-additive gene action was observed for most traits as reported by Hassan *et al* (2018), Ashish *et al* (2019), Inayat *et al* (2019) and Dezfouli *et al* (2019). Moreover, Genetic divergence between canola genotypes has considered the first step in the success of breeding program to

obtain more of new divergent recombination. In this regard, the genetic divergence between canola genotypes gave valuable heterosis and genetic variability in a study of Lefort-Buson *et al* (1985) who can be predicted it with several indicators of genetic divergence and Wolko *et al* (2019) who obtained the considered heterosis either positive or negative for studied traits based on genetic divergence between parents. Thus, precisely genetic information on inheritance of yield and yield-related traits in these breeding materials gives the best chance for formulating effective breeding and/or selection strategies to improve these traits in canola.

Therefore, the aims of this study were to determine types of combing ability and heterosis for seed weight plant⁻¹ and seed oil content, and to identify the inheritance of seed yield and yield-related traits by using Hayman's approach, and to estimate the proportion of dominant and recessive genes controlling these traits.

MATERIALS AND METHODS

Plant materials

Six genetically divergent parental canola genotypes in their agronomic traits were used in a half-diallel mating design (excluding reciprocal crosses) in the 2018/19 winter season at Kafr-El-Hamam/Sharkia Agricultural Research Station, Agricultural Research Center (ARC), Egypt, to generate 15 single-cross combinations. These parental canola genotypes were designed as N.A.36 (P1), N.A.37 (P2), N.A.38 (P3), N.A.39 (P4), N.A.14 (P5) and N.A.18 (P6) during conducted crosses program using a half-diallel mating design (Table1).

Table 1. Name, origin and description of canola parental genotypes

Parents	Origin	Days to 50% flowering	Plant height	Number of branches plant ⁻¹	Number of sili quae plant ⁻¹	1000-seed weight	Seed weight plant ⁻¹	Seed oil content	Erucic acid content
N.A.36	FAO	89.50	145.67	4.62	144.02	4.47	11.26	39.37	Low<2%
N.A.37	FAO	97.67	149.43	4.84	123.95	3.97	14.71	38.15	Low<2%
N.A.38	FAO	91.17	145.97	4.51	156.20	4.57	10.42	42.20	Low<2%
N.A.39	FAO	87.34	156.79	4.68	101.70	4.35	10.60	41.54	Low<2%
N.A.14	FAO	81.00	170.97	4.23	130.98	4.97	15.74	40.78	Low<2%
N.A.18	FAO	82.34	153.24	5.85	152.00	4.49	10.98	43.85	Low<2%

N.A.: Number of accessions and **FAO:** Food and Agricultural Organization.

On the other hand, their codes in GGE biplot were N.A.36, N.A.37, N.A.38, N.A.39, N.A.14 and N.A.18 for entries and N#A#36, N#A#37, N#A#38, N#A#39, N#A#14 and N#A#18 for testers. These breeding materials were obtained from the Oil Crops Research Department, Field Crops Research Institute, ARC, Egypt.

Soil samples of each site were analyzed to determine their compositions and chemical properties according to Jackson (1973) as given in Table 2.

Table 2. Soil composition and chemical properties of the upper 30 cm of the experimental soil for two experimental field stations.

Property	Sharkia/Kafr El Hamam	Etay-El-Baroud/Behaira
Soil composition		
Sand (%)	17.25	15.16
Silt (%)	35.36	32.27
Clay (%)	47.39	52.57
Soil texture	Clay loam	Clay
Chemical analysis		
Concentration of N (mg kg ⁻¹)	138	165
Concentration of P (mg kg ⁻¹)	7.26	8.95
Concentration of K (mg kg ⁻¹)	321	368
Electrical conductivity (ds/m)	0.32	1.23
pH	7.30	7.56

The previous crop at both locations was rice, which was planted in the summer season of 2019.

Planting, experimental design and cultural practices

In the subsequent winter season of 2019/20, the parents, along with their F1 crosses, were evaluated in a field experiment under irrigation conditions using a randomized complete block design with three replicates at Kafr El-Hamam/Sharkia and Etay-El-Baroud/Behaira Agricultural Research Stations, ARC, Egypt. The experimental plots consisted of two ridges, 5 m long and 60 cm wide, with a spacing of 10 cm between individual plants. Seeds of parents, along with their F1 crosses were hand-planted on adjacent plots. The seedlings were thinned to one plant per hill on one side of the ridge. The other cultural practices were followed as recommended by Oil Crops Research Department, Field Crops Research Institute, ARC, Egypt.

Data collection

Ten plants were randomly taken from each plot to measure plant height (cm), number of branches plant⁻¹, number of siliquae plant⁻¹, 1000-seed weight (g) and seed weight plant⁻¹ (g), which was adjusted to 15.5% seed moisture. Trait of days to 50% flowering was determined on a plot basis. Seed oil content was determined, after drying seed at 70°C for 48 h, by the Soxhlet extraction technique, using diethyl ether (AOAC, 1990).

Statistical analysis

Analysis of variance for combining ability according to method 2 model 1 of Griffing (1956) was done in each location for all studied traits. Moreover, Partitioning of dominance genetic effects (b) into three effects namely, b1 (test of mean deviation of F₁ from their mid-parental values), b2 (test of whether mean dominance deviation of the F₁ from their mid-parental values within each array differs over arrays), and b3 (test of dominance deviation that is unique to each F₁) was performed by analysis of Jones (1965) for each location. For identifying locations effects on genetic variance and its components, combined analysis was done after confirmed of homogeneity from the error variance as outlined by Steel *et al* (1997). General (GCA) and specific (SCA) combining ability effects, heterotic effects and the best crosses were determined through the GGE biplot software for seed weight plant⁻¹ and seed oil content at both locations (Yan, 2001). The genetic components, along with related genetic parameters were estimated as per Hayman's diallel analysis (Hayman, 1954b). Covariance

(W_r)/variance (V_r) graph of (Jinks 1954 and Hayman 1954a) was generated to determine the adequacy of the additive and dominance model and degree of dominance as well as the proportion of dominant and recessive alleles in the parental canola genotypes at two locations according to Efe (1995, 1996). Since, the adequacy of simple additive-dominance model was assessed by three scaling tests: uniformity of W_r and V_r (t2-test), joint regression analysis, and variance analysis of ($W_r + V_r$) and ($W_r - V_r$) for all studied traits at two locations. Failure or inadequacy of these three tests completely invalidates the additive-dominance model. However, if one of the tests fulfills the assumptions, the additive-dominance model is considered to be partially adequate.

However, either partially adequate or completely adequate types are considered indicators for further analysis to estimate the genetic components of variation (Johnson and Askel 1964 and Wilson *et al* 1978). Moreover, average degree of dominance can be obtained from the graphical display of parental variance (V_r) against parent offspring co-variance (W_r) analysis (W_r - V_r graph), as suggested by Mather and Jinks (1982). Statistical analyses, also, were carried out using MS-EXCEL (2007) with spreadsheet formula commands.

RESULTS AND DISCUSSION

1-Analysis of variance

There are highly significant variations among canola genotypes and their components i.e. parents, crosses and their interactions as revealed by individual locations (Table 3) and combined analysis across locations (Table 4) for all studied traits. This indicated that presence of adequate magnitude of genetic variability among studied materials, which allows estimating of genetic parameters for improving all studied traits. Similar results were reported by Elnenny *et al* (2015), Hassan *et al* (2018), Ashish *et al* (2019) and Dezfouli *et al* (2019). Highly significant differences were detected in locations and their interaction with genotypes and their components i.e. parents, crosses and their interactions for all studied traits. This indicated that evaluated locations possessed sufficient environmental differences resulted in differential responses of studied genotypes across locations.

Table 3. Mean squares of studied traits in six parental canola genotypes and their F1 crosses at Kafr El-Hamam (K) and Etay-El-Baroud (E) in the 2019/20 season.

SOV	df	Days to 50% flowering		Plant height		Number of branches plant ⁻¹		Number of siliquae plant ⁻¹	
		K	E	K	E	K	E	K	E
Rep.	2	1.2	0.4	9.81	6.3	0.4	0.03	33.9	7.34
Genotype	20	107.7 **	108.2 **	170.8 **	223.4 **	1.5 **	1.4 **	1200.2 **	1365.1 **
Parent (P)	5	101.7 **	125.0 **	252.6 **	295.6 **	0.9 **	1.2 **	1075.6 **	1453.3 **
Cross (C)	14	110.1 **	99.3 **	98.6 **	141.8 **	1.5 **	1.3 **	553.8 **	658.6 **
P VS C	1	104.8 **	149.6 **	772.9 **	1004.5 **	3.8 **	2.5 **	10873.4 **	10814.5 **
Error	40	0.96	0.90	4.92	5.50	0.13	0.10	19.42	18.05
SOV	df	1000-seed weight		Seed weight plant ⁻¹		Seed oil content			
		K	E	K	E	K	E		
Rep.	2	0.03	0.04	0.73	0.69	0.2	0.9		
Genotype	20	1.9 **	1.4 **	25.7 **	16.0 **	15.7 **	16.9 **		
Parent (P)	5	1.5 **	0.2*	16.1 **	16.6 **	13.6 **	11.6 **		
Cross (C)	14	1.1 **	0.6 **	16.7 **	6.0 **	10.2 **	14.0 **		
P VS C	1	15.5 **	18.9 **	199.5 **	154.0 **	104.2 **	84.6 **		
Error	40	0.04	0.05	0.43	0.42	0.3	0.3		

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 4. Mean squares in six parental canola genotypes and their F1 crosses for all studied traits across Kafr El-Hamam and Etay-El-Baroud in the 2019/20 winter season.

Source	df	Days to 50% flowering	Plant height	Number of branches plant ⁻¹	Number of siliquae plant ⁻¹	1000-seed weight	Seed weight plant ⁻¹	Seed oil content
Location (L)	1	2392.07**	20246.41**	9.35**	23446.61**	0.35**	31.19**	136.7**
Rep. x L	4	0.81	8.06	0.19	20.60	0.03	0.71	0.6
Genotypes (G)	20	53.42**	96.77**	0.63**	632.75**	0.65**	9.59**	7.6**
G x L	20	162.52**	297.39**	2.20**	1932.54**	2.64**	32.17**	25.0**
Parents (P)	5	56.13**	135.12**	0.47**	619.99**	0.16*	8.09**	6.2**
P x L	5	170.51**	413.08**	1.60**	1908.93**	1.48**	24.60**	18.9**
Crosses	14	51.76**	58.38**	0.62**	295.22**	0.26**	4.53**	5.3**
C x L	14	157.61**	181.96**	2.23**	917.15**	1.40**	18.21**	18.8**
P x C	1	63.11**	442.45**	1.55**	5421.98**	8.56**	87.99**	47.1**
P x C x L	1	191.33**	1334.92**	4.72**	16265.97**	25.76**	265.44**	141.7**
Error	80	0.93	5.21	0.12	18.73	0.05	0.43	0.3

*, ** Significant at 0.05 and 0.01 probability levels, respectively

2-Determination of genes controlling traits

Combining ability analysis is a common tool to identify genes controlling studied traits. This verified through its partitioning the genetic variations (Matzinger *et al* 1959) into general combining ability (GCA) which refers to additive gene effects (a) in Jones (1965) approach and specific combining ability (SCA) which refers to non-additive gene effects (b) in Jones (1965) approach. The highly significant differences due to GCA (a) and SCA (b) were detected in all studied traits for individual locations (Table 5) and combined analysis cross locations (Table 6), indicating the magnitude role of both additive and non-additive gene effects in the expression of all studied traits. This was confirmed for seed weight plant⁻¹ and seed oil content at both locations through GGE biplot (Figures 1a and 2f), since entries and testers had different projection on average tester coordinate (ATC) abscissa and ordinate for GCA and SCA effects, in the same order at both locations.

Table 5. Half diallel's analyses with Griffing method 2 model 1(1956) and Jones (1965) for all studied traits at Kafr-El-Hamam (K) and Etay-El-Baroud (E) in the 2019/20 winter season.

SOV		df	Days to 50% flowering		Plant height		Number of branches plant ⁻¹		Number of siliquae plant ⁻¹	
Griffing	Jones		K	E	K	E	K	E	K	E
Genotypes		20	35.91**	36.07**	56.94**	74.45**	0.48**	0.46**	400.08**	455.02**
GCA	a	5	108.28**	111.54**	70.17**	74.87**	0.26**	0.19**	481.49**	671.61**
SCA	b	15	11.79**	10.91**	52.53**	74.31**	0.56**	0.55**	372.94**	382.82**
	b1	1	34.95**	49.87**	257.63**	334.83**	1.25**	0.84**	3624.48**	3604.84**
	b2	5	5.61**	4.23**	24.50**	38.17**	0.92**	1.00**	139.07**	161.19**
	b3	9	12.65**	10.30**	45.31**	65.44**	0.28**	0.26**	141.59**	147.95**
Error		40	0.32	0.30	1.64	1.83	0.04	0.03	6.47	6.02
SOV		df	1000-seed weight		Seed weight plant ⁻¹		Seed oil content			
			K	E	K	E	K	E		
Genotypes		20	0.63**	0.47**	8.57**	5.35**	5.23**	5.64**		
GCA	a	5	0.38**	0.17**	4.46**	2.83**	6.1**	3.6**		
SCA	b	15	0.71**	0.57**	9.94**	6.19**	5.0**	6.3**		
	b1	1	5.15**	6.29**	66.49**	51.32**	34.7**	28.2**		
	b2	5	0.41**	0.06*	6.73**	3.92**	2.4**	4.7**		
	b3	9	0.38**	0.21**	5.444**	2.43**	3.1**	4.8**		
Error		40	0.01	0.02	0.14	0.14	0.09	0.12		

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

Table 6. Half diallel's analyses with Griffing method 2 model 1 (1956) and Jones (1965) for all studied traits across Kafr-El-Hamam (K) and Etay-El-Baroud (E) in the 2019/20 winter season.

SOV		df	Days to 50% flowering	Plant height	Number of branches plant ⁻¹	Number of siliquae plant ⁻¹	1000-seed weight	Seed weight plant ⁻¹	Seed oil content
Griffing	Jones								
Location (L)		1	797.36**	6748.80**	3.12**	7815.54**	0.12**	10.40**	45.58**
Rep. x L		4	0.27	2.69	0.06	6.87	0.01	0.24	0.20
Genotypes		20	17.81**	32.26**	0.21**	210.92**	0.22**	3.20**	2.55**
GCA	a	4	219.28**	141.22**	0.34**	1131.20**	0.19**	6.08**	9.04**
SCA	b	10	21.88**	124.96**	1.00**	747.82**	1.09**	15.03**	10.56**
	b1	1	84.15**	589.93**	2.07**	7229.30**	11.41**	117.32**	62.76**
	b2	4	9.11**	61.38**	1.90**	292.92**	0.30**	9.11**	6.79**
	b3	5	22.06**	108.62**	0.38**	280.37**	0.39**	6.95**	6.86**
GCA x L	a x L	4	0.54	3.83	0.11*	21.90**	0.37**	1.21**	0.61**
SCA x L	b*L	10	0.82**	1.87	0.10**	7.94	0.18**	1.10**	0.72**
	b1*L	1	0.66	2.53	0.02	0.01	0.028	0.49006	0.17
	b2*L	4	0.73*	1.29	0.02	7.33	0.17**	1.53**	0.34**
	b3*L	5	0.89**	2.13	0.16**	9.16	0.21**	0.9330**	1.00**
Error		80	0.31	1.74	0.04	6.24	0.02	0.14	0.10

*, ** Significant at 0.05 and 0.01 probability levels, respectively.

However, a GCA (a)/SCA (b) ratio being greater than 60% was detected for days to 50% flowering, plant height and number of siliquae plant⁻¹ at both individual locations and across locations and seed oil content at Kafr-El-Hamam, revealing that the inheritance of these traits were governed by additive and additive x additive gene effects, although dominance and over-dominance gene effects was also contributed in the genetic system of control of these traits. Similar findings were reported by Hassan *et al* (2018), Ashish *et al* (2019) and Dezfouli *et al* (2019) also stated both additive and non-additive gene actions were important in the expression of investigated traits and preponderance of non-additive gene action was observed for most traits.

In Jones (1965) approach, the significance of directional dominance (b1) signifies the presence of directional dominance with the preponderance of additive gene action for all studied traits only at individual locations (Tables 5 and 6). The significance of distribution of dominant and recessive alleles in parents (b2) for all studied traits at both individual locations and some of them in combined analysis, showed the presence of asymmetrical

distribution of dominant and recessive genes in parents. Specific gene interactions or epistasis was detected for all studied traits at both individual location and most of them across locations, as revealed by the significance of dominance deviation unique to F_1 s (b3). Moreover, significant interactions of locations with both of additive (GCA) or non-additive (SCA) gene effects were detected in most studied traits (Table 6). This indicated that selection of different parental canola genotypes and specific cross combinations was necessary for developing new recombination specific for each location.

4-GGE biplot analysis for half diallel data.

4-1-Combining ability effects

The biplot of 1st and 2nd principal component analysis for seed weight plant⁻¹ (Figure 1 a-f) and seed oil content (Figure 2 a-f) explained 79.6% and 78.9% at Kafr-El-Hamam and 74.4% and 86.7% at Etay-El-Baroud, respectively. This clearly indicated that GGE biplot had the largest proportion of the variation, hence it was more effectively in the graphical analysis for these traits. In this respect, Ghani *et al* (2016) found that graphic of the GGE biplot graphic was a rapid and effective tool for estimating general combining ability and specific combining ability effects of parental breeding materials and their crosses. The ATC abscissa arrow had been divided into two directions, positive as one direction and negative as another one by the double headed-arrow arrow (ATC ordinate). Where, the positive direction is the same direction of ATC abscissa, but the negative is the opposite direction. The highest general combining ability effects approximated with direction of ATC abscissa or with the largest projection on the ATC abscissa and *vice versa*.

The good general combiners for producing the heaviest weight of seed plant⁻¹ were detected in the entry N.A.36 and N.A.39 at Kafr-El-Hamam (Fig. 1a A1) and N.A.39 and N.A.14 at Etay-El-Baroud (Fig. 1d A1), as they located far from the origin point in the direction of the ATC abscissa (most discriminate). In case of seed oil content, the parents N.A.36, N.A.38 and N.A.39 at Kafr-El-Hamam (Fig. 2a B1) and N.A.36, N.A.39 and N.A.14 at Etay-El-Baroud (Fig.2d B1) had the highest GCA effects, as they had the largest projection on the ATC abscissa. However, the largest projection of entries on the ATC ordinate (most representatives)

approximated with their SCA effects. Hence, the parents N.A.39, N.A.36 and N.A.18 at Kafr-El-Hamam and N.A.38 and N.A.39 at Etay-El-Baroud had the highest SCA effects for seed weight plant⁻¹, as they had the largest projection on ATC ordinate (most representatives). The parents N.A.39, N.A.14, N.A.38 and N.A.37 at Kafr-ElHamam and N.A.39, N.A.14, N.A.36 and N.A.37 at Etay-El-Baroud were categorized as the best specific combiners for seed oil content, as they had the largest projection on ATC ordinate. In the study of Inayat *et al* (2019) found that combining ability effects were positive on seed weight plant⁻¹ and seed oil content.

4-2-Heterotic effects

The testers can be grouped by PCA2 scores (Yan and Hunt, 2002). The testers were divided to three groups, the testers N.A.36 and N.A.37 for seed weight plant⁻¹ at Kafr-El-Hamam (Fig. 1b A2) as well as N.A.37 for seed weight plant⁻¹ (Fig. 1e A2) and N.A.18 for seed oil content (Fig. 2e B2) at Etay-El-Baroud located above PCA2 guideline as first group. The second group included tester N.A.38 and N.A.14 for seed weight plant⁻¹ at both locations as well as N.A.37, N.A.38 and N.A.18 at Kafr-El-Hamam and N.A.37 and N.A.38 at Etay-El-Baroud for seed oil content occupied below PCA2 guideline. Whereas, the other testers for seed weight plant⁻¹ and seed oil content at both locations had negative scores for PCA1, hence did not seem to belong to either positive heterotic group. Moreover, the testers in the first group interacted positively with entries located above PCA2 guideline for seed weight plant⁻¹ and seed oil content at both locations but they negatively interacted among themselves. Similarly, the testers in the second group interacted positively with the entries located below PCA2 guideline but they negatively interacted with themselves. The considerable heterosis was detected among first and second groups, indicated that interactions of dominant genes among these parents in these two groups resulted in over-dominance or epistatic effect. The results of Luo *et al* (2019) revealed mating among intra-group parents gave higher heterotic hybrids in *brassica napus* than better parents, which was consistent with the current results.

4-3-Best crosses

The polygon view was divided by perpendicular lines into three well defined sectors, of which corner entry N.A.38 was a good mating partner

with tester N.A.39, entry N.A.36 with tester N.A.18, and entries N.A.39 and N.A.18 with testers N.A.38, N.A.14 and N.A.37 for seed weight plant⁻¹ at Kafr-El-Hamam (Fig.1c A3), four sectors of which vertex entry N.A.39 was the best mating partner with tester N.A.38, entry N.A.18 with tester N.A.14, entry N.A.38 with tester N.A.39 and entry N.A.14 with testers N.A.18 and N.A.36 at Etay-El-Baroud (Fig.1f A3). Superior heterotic crosses were detected in seed oil content, since the perpendicular lines divided polygon into five sectors, of which vertex entry N.A.39 was the best mating partner with tester N.A.37 and N.A.38, entry N.A.37 with tester N.A.36, entry 38 with tester N.A.14 and N.A.39, entry N.A.36 with tester N.A.18 for seed oil content at Kafr-El-Hamam (Fig.2c B3), three sectors of which corner entry N.A.39 along with N.A.14 was the best mating partners with testers N.A.18, N.A.37, N.A.38 and N.A.36, entry 37 with tester N.A.14, entry N.A.36 with N.A.39 at Etay-El-Baroud (Fig.2f B3). These finding is in accordance with the findings of Hassan *et al* (2018) and Ashish *et al* (2019) that reported to some extent the same kind of results.

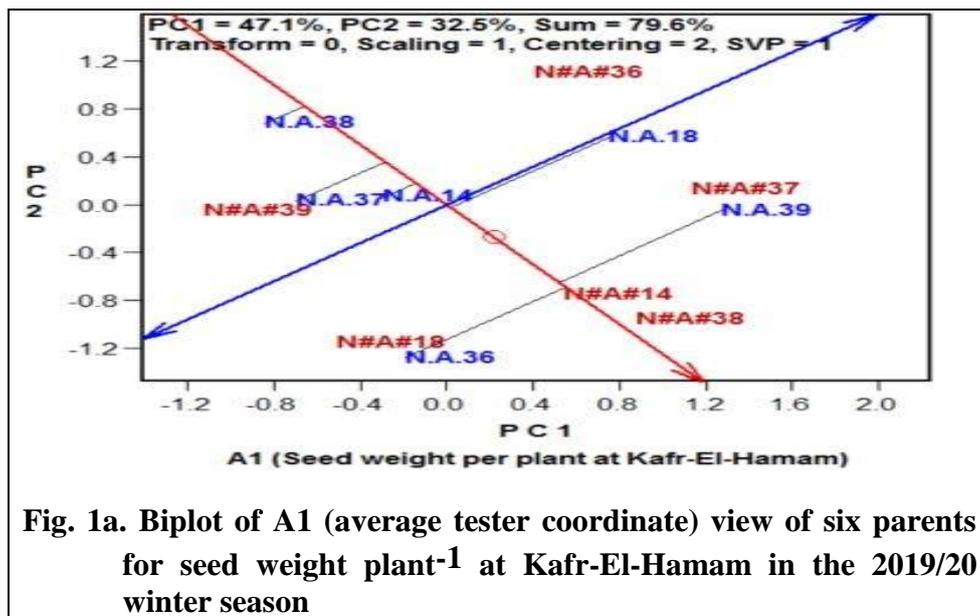


Fig. 1a. Biplot of A1 (average tester coordinate) view of six parents for seed weight plant⁻¹ at Kafr-El-Hamam in the 2019/20 winter season

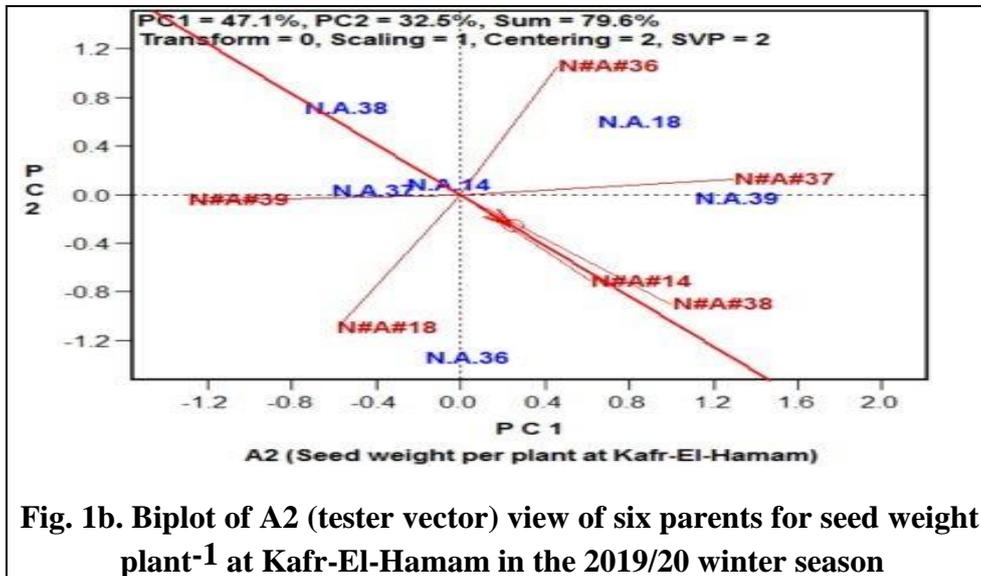


Fig. 1b. Biplot of A2 (tester vector) view of six parents for seed weight plant⁻¹ at Kafr-El-Hamam in the 2019/20 winter season

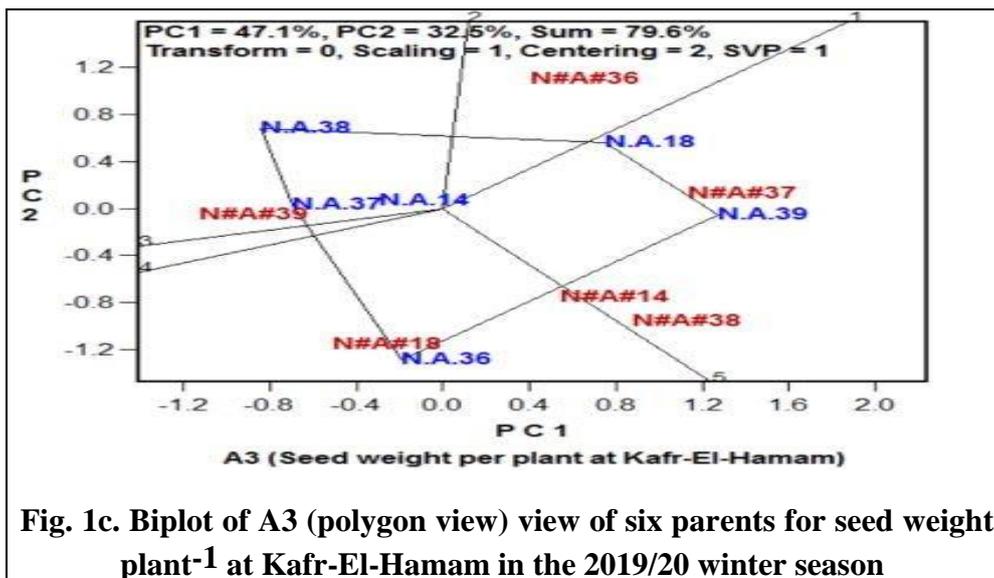
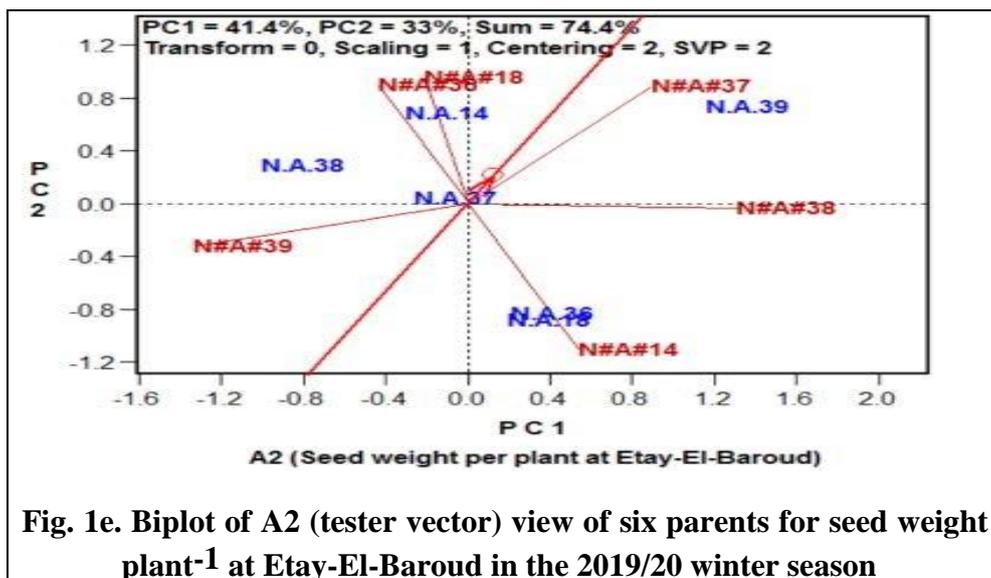
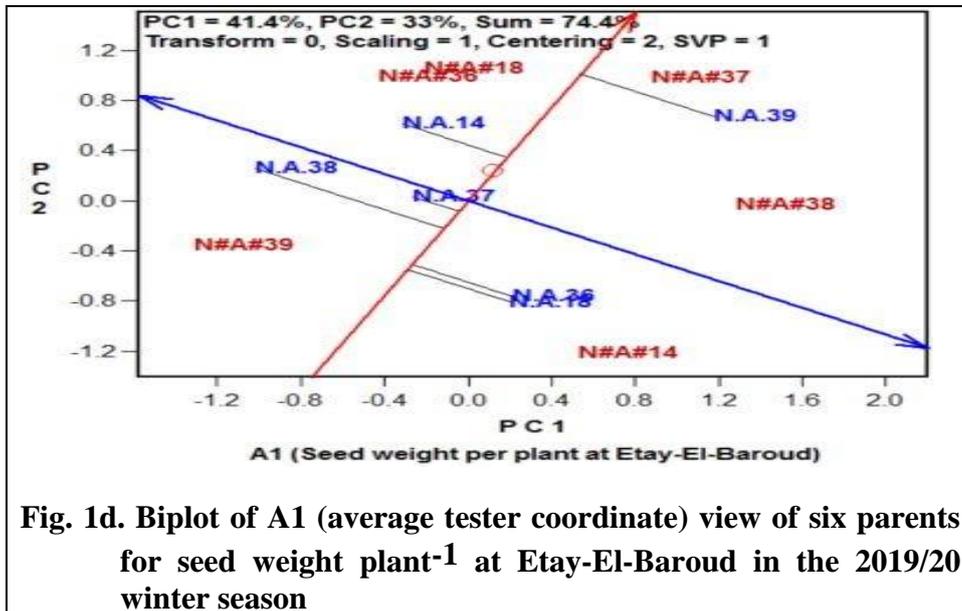


Fig. 1c. Biplot of A3 (polygon view) view of six parents for seed weight plant⁻¹ at Kafr-El-Hamam in the 2019/20 winter season



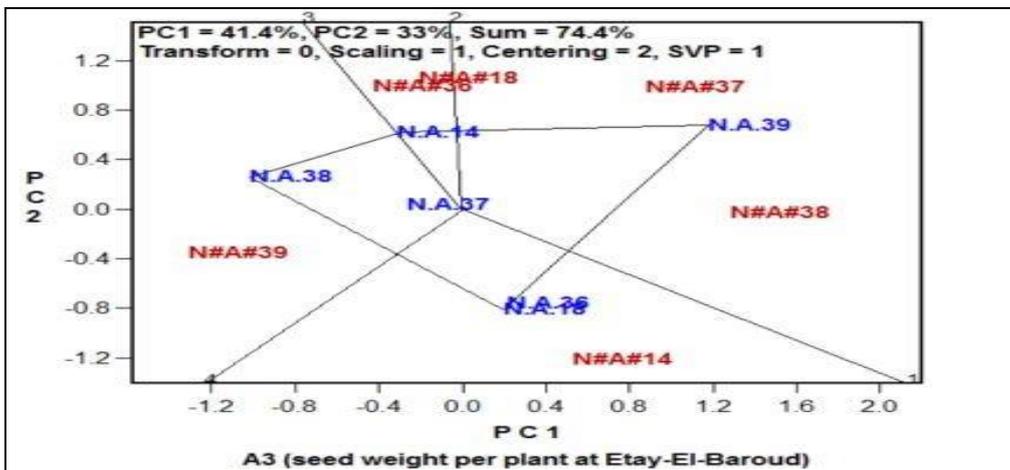


Fig. 1f. Biplot of A3 (polygon view) view of six parents for seed weight plant⁻¹ at Etay-El-Baroud in the 2019/20 winter season

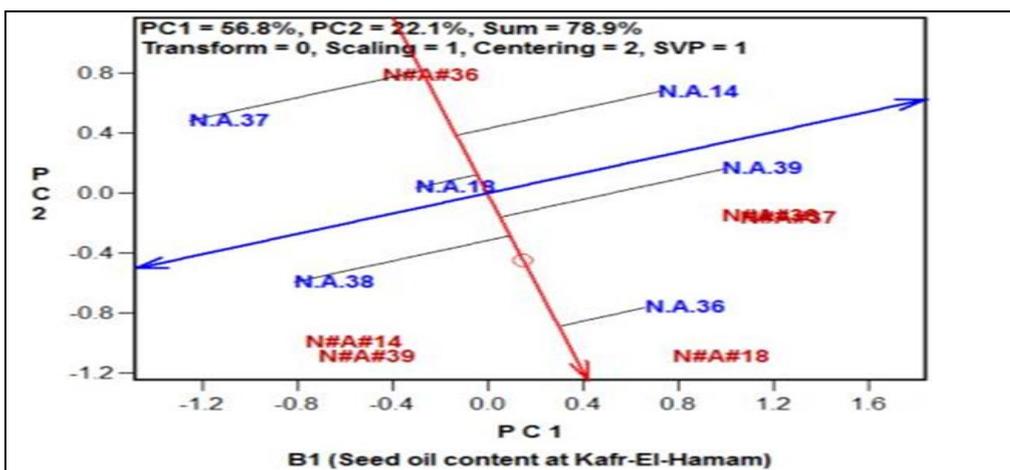
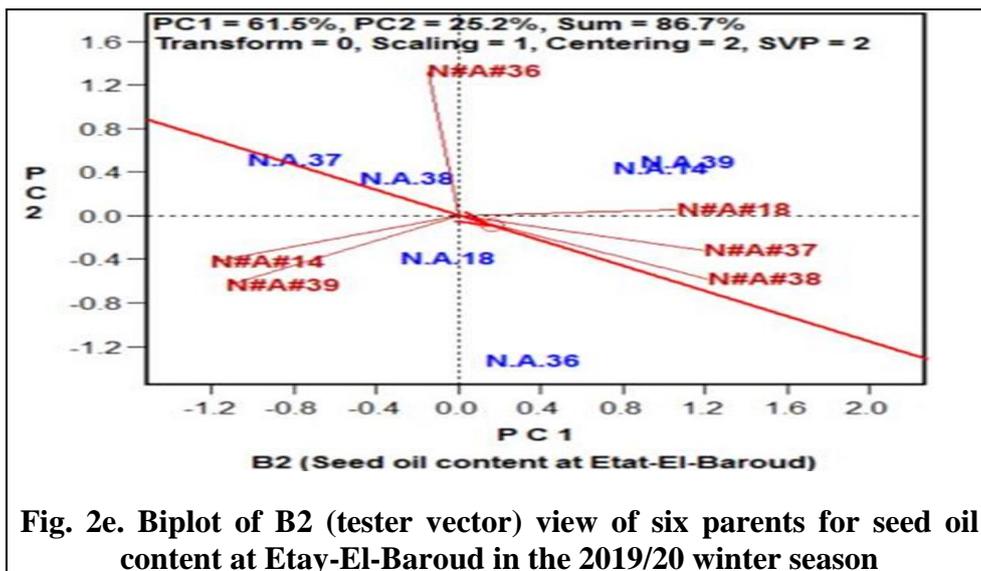
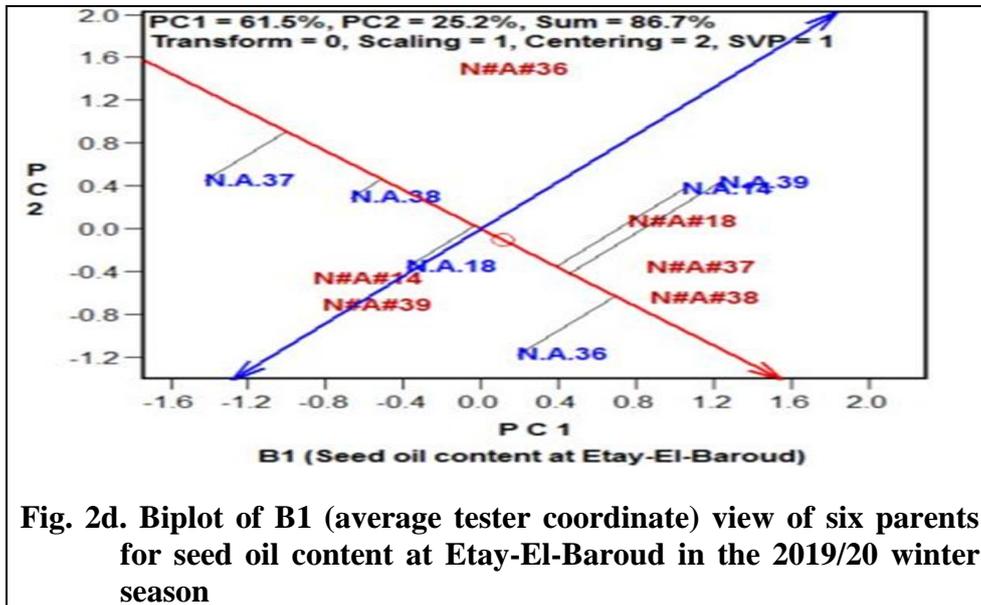


Fig. 2a. Biplot of B1 (average tester coordinate) view of six parents for seed oil content at Kafr-El-Hamam in the 2019/20 winter season



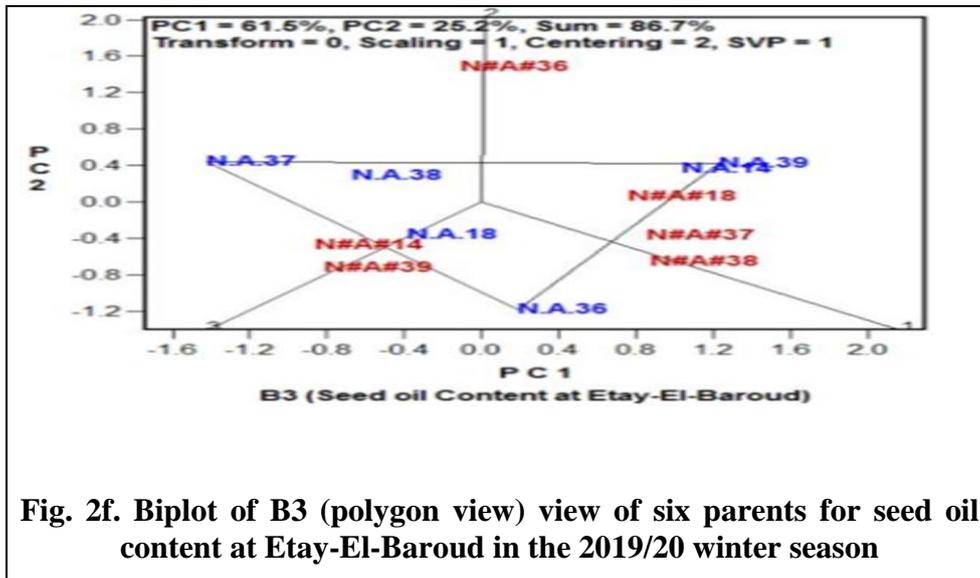


Fig. 2f. Biplot of B3 (polygon view) view of six parents for seed oil content at Etay-El-Baroud in the 2019/20 winter season

3-Hayman numerical and graphical analysis

3-1-Adequacy of additive-dominance model

Results of all tests revealed that the validity of the additive-dominance model varied from partially to fully adequate (Table 7); thus further analysis of data for determination of genetic components according to Hayman (1954b) was ensured.

3-2-Genetic components and their ratios

As revealed from graphical analyses (Figure 3–16), the regression line intercepted the covariance axis below the point of origin in all studied traits at both locations (except for days to 50% flowering, number of branches plant⁻¹ and seed oil content at both individual locations), indicating that over-dominance was involved in controlling these traits. This was further confirmed by the average degree of dominance $(H1/D)^{0.5}$ (Table 8), which was more than unity for all studied traits (except for days to 50% flowering at Etay-El-Baroud) and indicated the involvement of over dominance.

Table 7. Adequacy test of the data for additive-dominance model for all studied traits at Kafr-El-Hamam (K) and Etay-El-Baroud (E) in the 2019/20 winter season.

Traits	†L	t ²	Joint regression analysis			Analysis of variance of array	
			(b)±SE	b=0	b=1	Wr+Vr	Wr-Vr
Days to 50% flowering	K	NS‡	0.75±0.14	5.21**	1.71	**	**
	E	NS	0.98±0.05	21.69**	0.41	**	NS
Plant height	K	NS	1.02±0.48	2.11	-0.04	**	**
	E	NS	0.66±0.44	1.49	0.77	**	**
Number of branches plant ⁻¹	K	NS	-0.47±0.67	-0.71	2.20	**	**
	E	NS	-0.46±0.43	-1.07	3.40*	**	**
Number of siliquae plant ⁻¹	K	NS	0.69±0.23	3.00*	1.34	**	**
	E	NS	0.92±0.16	5.62**	0.51	**	**
1000-seed weight	K	NS	0.33±0.28	1.16	2.38	**	**
	E	NS	0.13±0.26	0.49	3.30*	**	**
Seed weight plant ⁻¹	K	NS	0.57±0.19	2.92*	2.24	**	**
	E	NS	0.48±0.26	1.90	2.02	**	**
Seed oil content	K	NS	0.14±0.30	0.48	2.86*	**	**
	E	NS	-0.07±0.26	-0.27	4.14*	**	**

†L = Location; *, ** Significant at 0.05 and 0.01 probability levels, respectively; ‡NS = Non-significant. b: regression coefficient; b=0: deviation of regression coefficient from zero; b=1: deviation of regression coefficient from unit.

The significance of additive (a) and non-additive (b) effects in Jones (1965) analysis (Table 8) and additive (D) and two dominance types in Hayman (1954b) analysis (Table 8) indicated the importance of both additive and non-additive genetic components in the inheritance of all studied traits at both locations. However, the larger magnitude of dominance gene action compared with additive gene action (which was also confirmed by ratio a/b being lesser than unity for all studied traits, except for days to 50% flowering, plant height and number of siliquae plant⁻¹ at both individual locations and across locations and seed oil content at Kafr El-Hamam.

Table 8. Components of the genetic variance and their ratios (Hayman 1954b) for all studied traits at Kafr El-Hamam (K) and Etay-El-Baroud (E) in the 2019/20 winter season.

Item	†L	Days to 50% flowering	Plant height	Number of branches plant ⁻¹	Number of siliquae plant ⁻¹	1000-seed weight	Seed weight plant ⁻¹	Seed oil content
E	K	0.32	1.72	0.05	6.70	0.01	0.15	0.09
	E	0.29	1.85	0.03	5.85	0.02	0.14	0.13
D	K	33.56**	82.49**	0.24	351.83**	0.47	5.21**	4.43**
	E	41.37**	96.69**	0.37	478.59**	0.04	5.40**	3.73
F	K	-23.70	79.53	0.75	240.83	0.65	8.45*	3.49
	E	-16.38	104.45	1.04	297.84*	-0.02	7.92*	5.72
H1	K	44.91**	187.78**	2.37**	1132.99**	2.41**	34.98**	16.83**
	E	39.21**	272.08**	2.45**	1186.78**	1.54**	20.41**	23.93**
H2	K	40.14**	167.15**	1.59**	1013.84**	2.05**	29.09**	14.74**
	E	35.65**	239.38**	1.59*	1047.41**	1.51**	17.02**	19.83**
h2	K	22.47**	166.03**	0.78*	2345.47**	3.33**	43.01**	22.46**
	E	32.16**	215.99**	0.53	2333.22**	4.07**	33.18**	18.21**
(H1/D) ^{0.5}	K	1.16	1.51	3.17	1.79	2.26	2.59	1.95
	E	0.97	1.68	2.57	1.57	6.04	1.94	2.53
H ₂ /4H ₁	K	0.22	0.22	0.17	0.22	0.21	0.21	0.22
	E	0.23	0.22	0.16	0.22	0.24	0.21	0.21
KD/KR	K	0.53	1.94	3.01	1.47	1.87	1.91	1.51
	E	0.66	1.95	3.37	1.49	0.91	2.21	1.87
R	K	0.07NS	0.98**	0.08NS	-0.95**	-0.827*	-0.61NS	-0.16NS
	E	-0.106NS	0.92**	0.34NS	-0.96**	-0.33NS	-0.93**	-0.09NS
h2/H2	K	0.56	0.99	0.49	2.31	1.62	1.48	1.52
	E	0.90	0.90	0.33	2.23	2.70	1.95	0.92
h ² (n.s)	K	0.75	0.21	0.23	0.31	0.15	0.15	0.29
	E	0.77	0.17	0.19	0.37	0.12	0.09	0.17
H ² (b.s)	K	0.99	0.97	0.92	0.98	0.98	0.98	0.98
	E	0.99	0.98	0.94	0.99	0.96	0.97	0.98

*, ** Significant at 0.05 and 0.01 probability level, respectively; †L = Location.

This was further supported by low narrow sense heritability (Table 8) for all studied traits except for days to 50% flowering (0.75 at Kafr-El-Hamam and 0.77 at Etay-El-Baroud). These results are in line with the findings of Hassan *et al* (2018), Ashish *et al* (2019) and Dezfouli *et al* (2019). Consequently, the simple selection of superior segregates in late generations would be effective for improving most of the studied traits. Considerable differences between H1 and H2 dominance types (Table 8) were detected for all studied traits at both locations. This showed an unequal distribution of dominant and recessive genes in the parents, which was also verified by the H2/4H1 ratio (Table 8). The ratios were less than the maximum value (0.25) for all studied traits. The positive F value (Table 8) of all studied traits (except for days to 50% flowering at both individual locations, and 1000-seed weight at Etay-El-Baroud) suggested that the frequency of dominant alleles was more larger than that of the recessive alleles in the parents, and this was further supported by the ratio of KD/KR, which was more than unity at both locations except for days to 50% flowering at both locations. The values of h²/H² (Table 8), which represent the number of gene pairs controlling the studied traits, were computed.

These values indicated that one to two pairs of dominant genes governed the inheritance of all studied traits at both locations. Same results were obtained by Gul *et al* (2019) who revealed that non-additive gene action was preponderance in the inheritance of all studied traits and hence, the delayed selection in later segregating generations might be more effective.

5-Distribution of dominant and recessive genes among the parents

Parental canola genotypes widely scattered in the Wr-Vr graphical analysis for all studied traits at both locations, this confirmed their genetic diversity. Correlation of dominance parental order (Wr+Vr) with parental measurements was positive for days to 50% flowering and plant height in most cases, indicating recessive genes contributed toward a positive direction.

The desirable parents (Table 9 and Figures 3-16) that possessed negative/decreasing-effect recessive (-Ri)/dominant (-Di) genes were detected in N.A.39 (with -Ri 88.32% and 89.58%), N.A.14 (with -Ri

57.01% and 61.90%) and N.A.18 (with -Di 57.58% and 58.36%) for early flowering, N.A.36 (with -Di 93.55% and 93.19%), N.A.37 (with -Di 84.65% and 84.12%) and N.A.38 (with -Di 82.64% and 74.74%) for short plant stature at Kafr-El-Hamam and Etay-El-Baroud, respectively.

Table 9. Percentage of recessive (Ri%) and dominant (Di%) genes in parental canola genotypes for all studied traits at Kafr-El-Hamam (K) and Etay-El-Baroud (E) in the 2019/20 winter season.

Parents	Days to 50% flowering				Plant height				Number of branches plant ⁻¹				Number of siliquae plant ⁻¹			
	K		E		K		E		K		E		K		E	
	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%
N.A.36	38.36	61.64	58.20	41.80	93.55	6.45	93.19	6.81	77.85	22.15	71.98	28.02	61.57	38.43	71.50	28.50
N.A.37	56.11	43.89	57.79	42.21	84.65	15.35	84.12	15.88	80.94	19.06	86.77	13.23	53.26	46.74	52.61	47.39
N.A.38	4.65	95.35	18.35	81.65	82.64	17.36	74.74	25.26	91.81	8.19	81.09	18.91	80.73	19.27	78.63	21.37
N.A.39	11.68	88.32	10.42	89.58	57.75	42.25	74.12	25.88	66.77	33.23	89.18	10.82	24.02	75.98	7.35	92.65
N.A.14	42.99	57.01	38.10	61.90	16.17	83.83	17.52	82.48	61.18	38.82	68.88	31.12	59.08	40.92	70.08	29.92
N.A.18	57.58	42.42	58.36	41.64	61.66	38.34	53.38	46.62	66.58	33.42	62.04	37.96	79.65	20.35	79.89	20.11
Parents	1000-seed weight				Seed weight plant ⁻¹				Seed oil content							
	K		E		K		E		K		E					
	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%	Di%	Ri%				
N.A.36	66.65	33.35	57.61	42.39	44.86	55.14	70.60	29.40	49.63	50.37	68.90	31.10				
N.A.37	9.15	90.85	50.24	49.76	87.91	12.09	90.54	9.46	53.79	46.21	41.88	58.12				
N.A.38	74.88	25.12	73.83	26.17	80.04	19.96	60.72	39.28	48.83	51.17	63.47	36.53				
N.A.39	64.33	35.67	25.13	74.87	59.30	40.70	55.30	44.70	62.00	38.00	78.54	21.46				
N.A.14	93.22	6.78	39.97	60.03	79.91	20.09	88.14	11.86	82.68	17.32	89.42	10.58				
N.A.18	83.51	16.49	52.79	47.21	42.28	57.72	48.11	51.89	64.59	35.41	49.13	50.87				

Correlation of dominance parental order with parental measurements was negative and considerable (Table 9 and Figures 3–16) for remaining traits except for number of branches plant⁻¹ at both locations, indicating that a proportion of recessive alleles was higher with positive effects than dominant alleles for these traits. The preferred parents (Table 9 and Figures 3-16) were observed in N.A.18 (with +Ri 33.42% and 37.96%) at Kafr-El-Hamam and Etay-El-Baroud, respectively and N.A.37 (with +Ri 13.23%) at Etay-El-Baroud for number of branches plant⁻¹, N.A.36 (with +Di 61.57% and 71.50%), N.A.38 (with +Di 80.73 % and 78.63 %) and N.A.18 (with +Di 79.65% and 79.89%) for number of siliquae plant⁻¹ at Kafr-El-Hamam and Etay-El-Baroud, respectively, N.A.14 (with +Di 93.22%) and N.A.18 (with +Di 83.51%) at Kafr-El-Hamam and N.A.36 (with +Di 57.61%) and N.A.38 (with +Di 73.83%) at Etay-El-Baroud for thousand seed weight

plant⁻¹, N.A.37 (with +Di 87.91% and 90.54%) and N.A.14 (with +Di 79.91% and 88.14%) at Kafr-El-Hamam and Etay-El-Baroud, respectively for increasing seed weight plant⁻¹ and N.A.39 (with +Di 62.00% and 78.54%) at Kafr-El-Hamam and Etay-El-Baroud, respectively, N.A.18 (with +Di 64.59%) at Kafr-El-Hamam and N.A.14 (with +Di 89.42%) at Etay-El-Baroud for increasing proportion of seed oil.

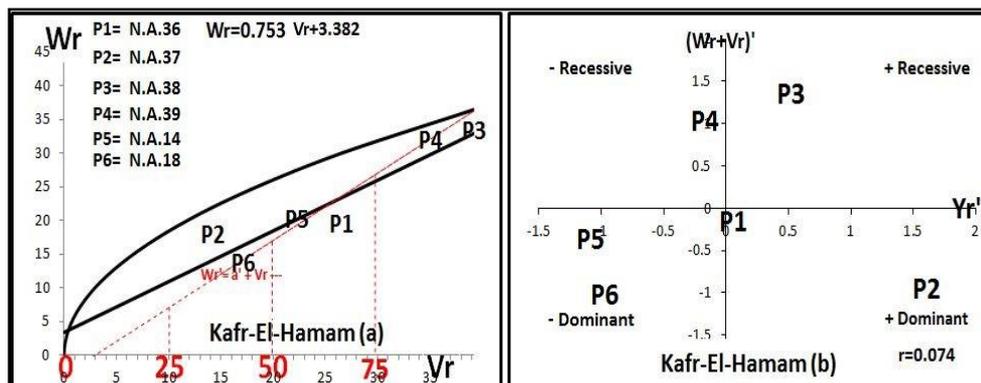


Fig. 3. W_r - V_r (a) and standardized deviations (b) graphs for days to 50% flowering at Kafr-El-Hamam.

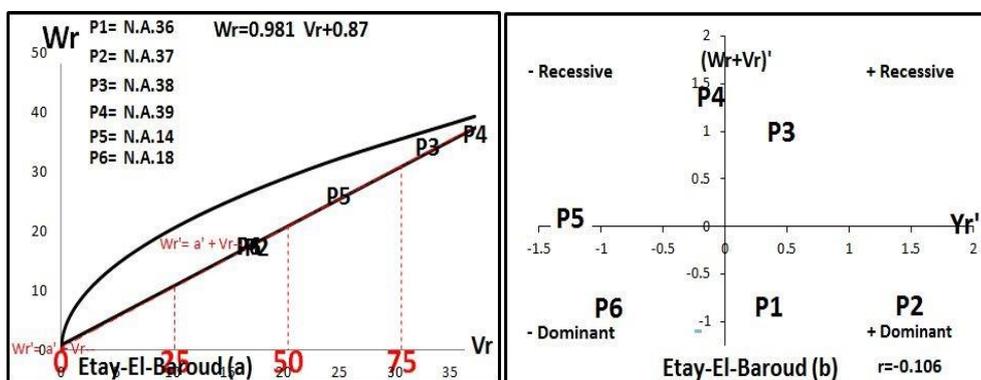


Fig. 4. W_r - V_r (a) and standardized deviations (b) graphs for days to 50% flowering at Etay-El-Baroud.

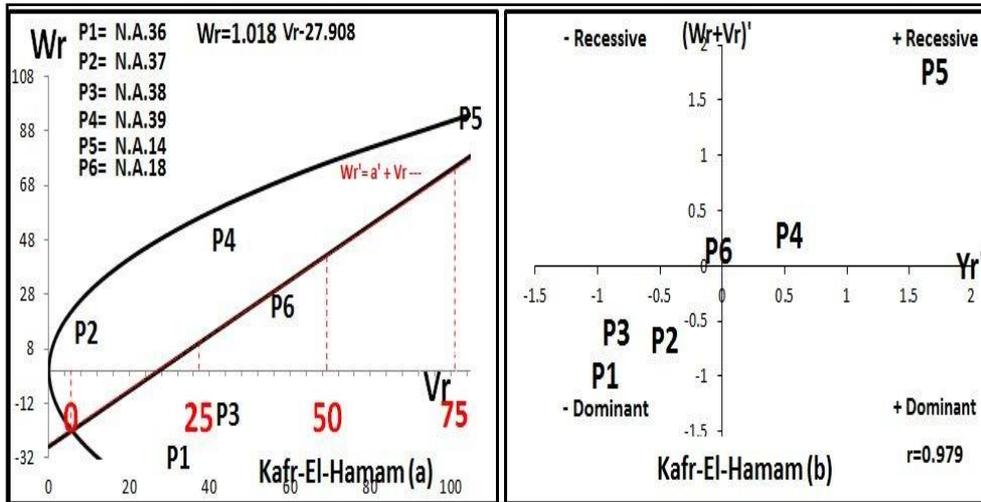


Fig. 5. Wr - Vr (a) and standardized deviations (b) graphs for plant height at Kafr-El-Hamam.

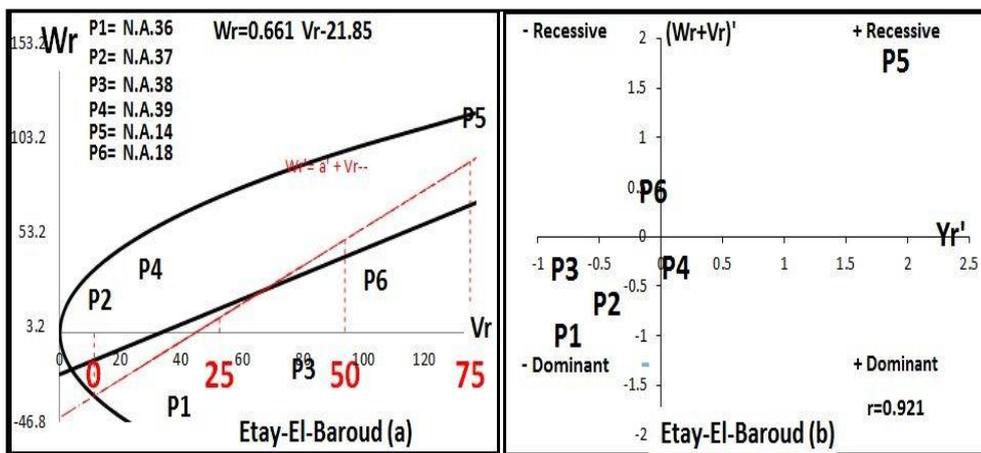


Fig. 6. Wr - Vr (a) and standardized deviations (b) graphs for plant height at Etay-El-Baroud.

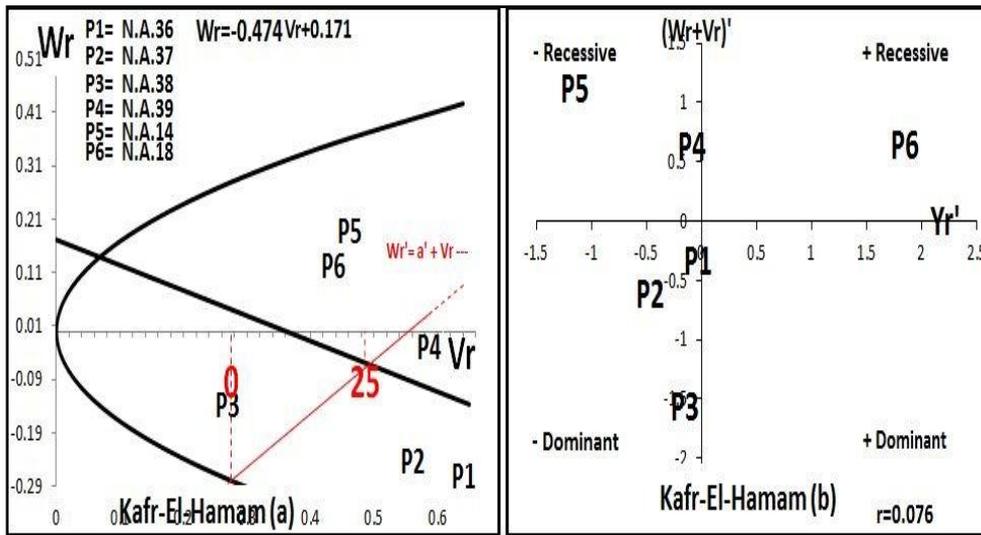


Fig. 7. W_r - V_r (a) and standardized deviations (b) graphs for number of branches plant⁻¹ at Kafr-El-Hamam.

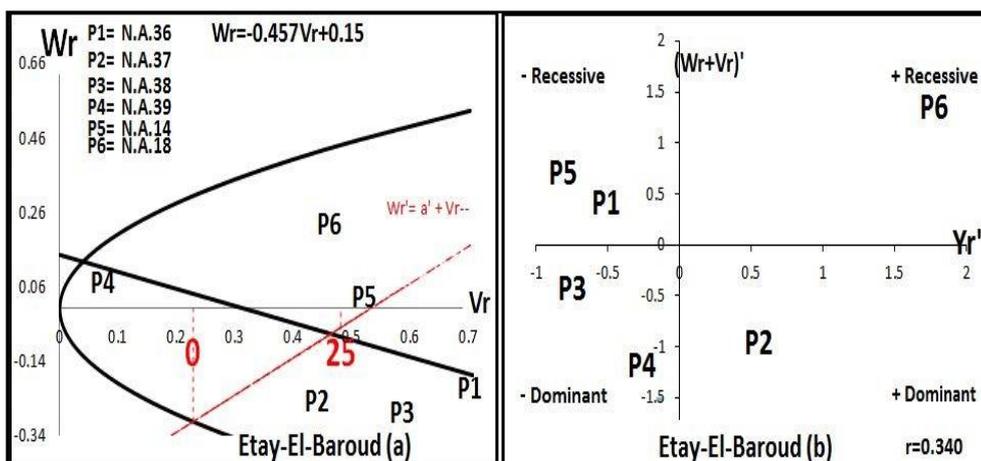


Fig. 8. W_r - V_r (a) and standardized deviations (b) graphs for number of branches plant⁻¹ at Etay-El-Baroud.

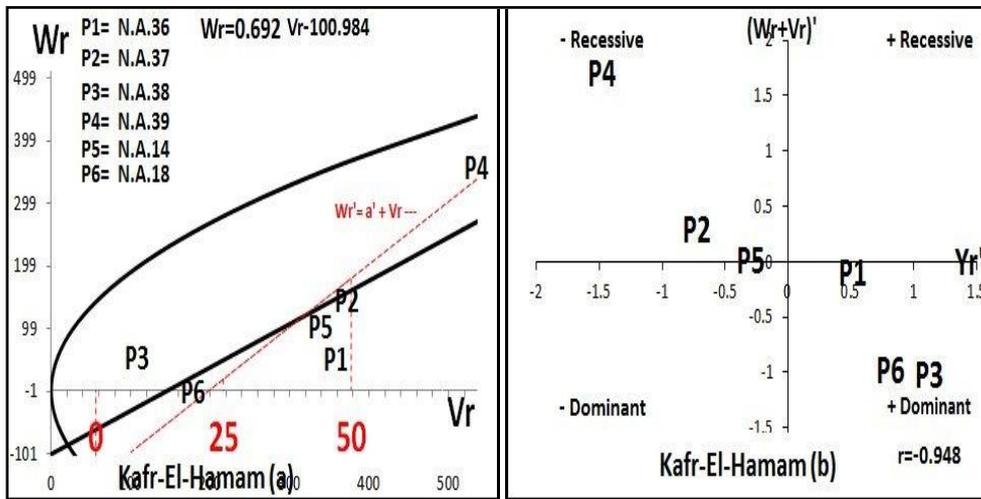


Fig. 9. Wr-Vr (a) and standardized deviations (b) graphs for number of siliquae plant⁻¹ at Kafr-El-Hamam.

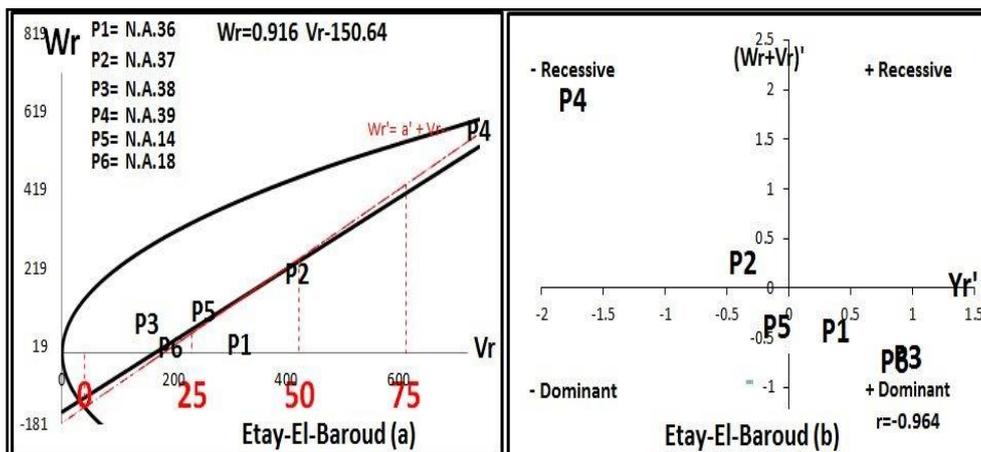


Fig. 10. Wr-Vr (a) and standardized deviations (b) graphs for number of siliquae plant⁻¹ at Etay-El-Baroud.

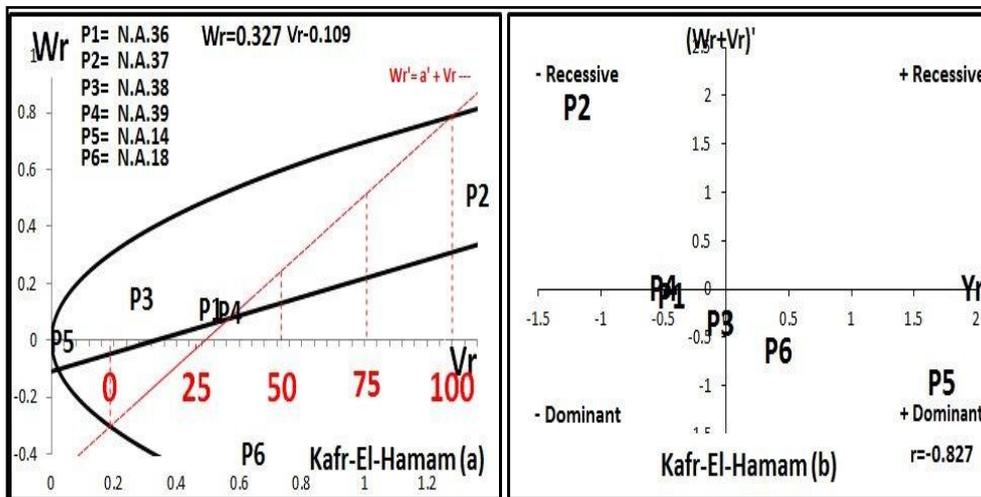


Fig. 11. W_r - V_r (a) and standardized deviations (b) graphs for 1000-seed weight at Kafr-El-Hamam.

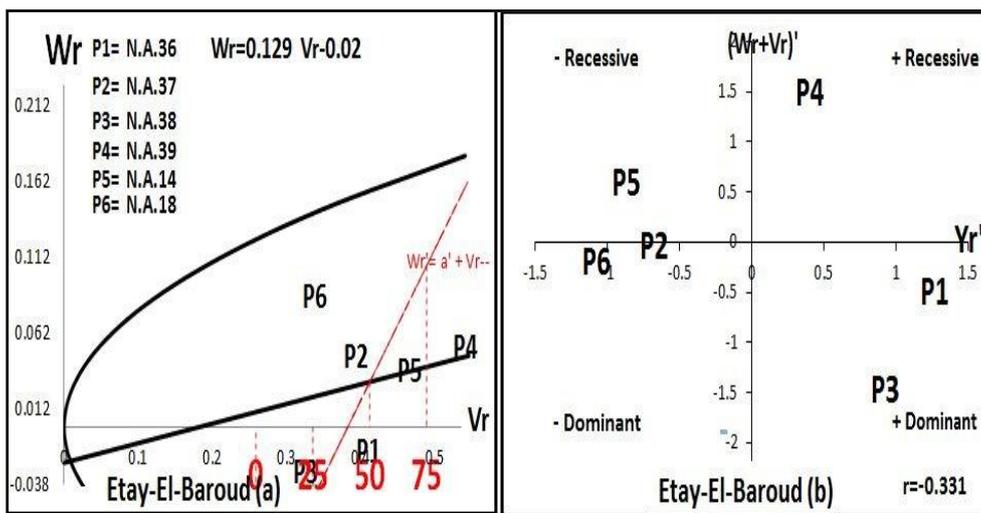


Fig. 12. W_r - V_r (a) and standardized deviations (b) graphs for 1000-seed weight at Etay-El-Baroud.

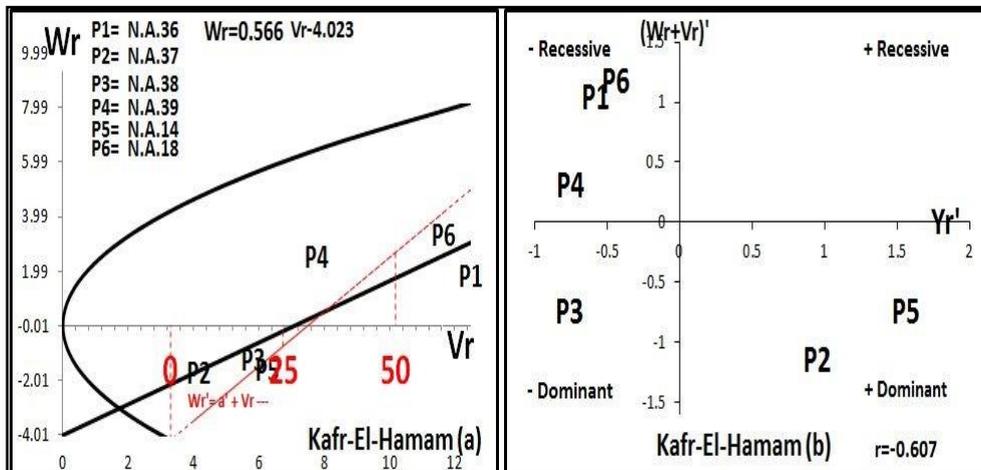


Fig. 13. Wr - Vr (a) and standardized deviations (b) graphs for seed weight plant⁻¹ at Kafr-El-Hamam.

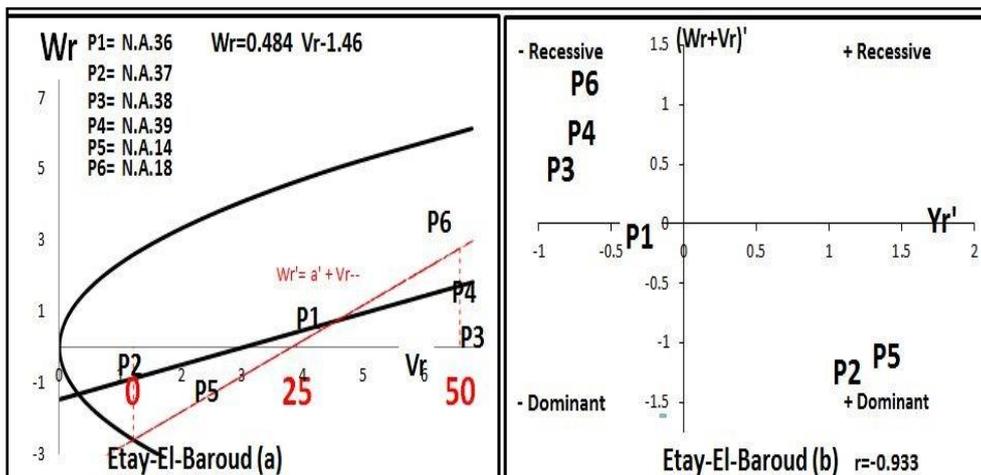


Fig. 14. Wr - Vr (a) and standardized deviations (b) graphs for seed weight plant⁻¹ at Etay-El-Baroud.

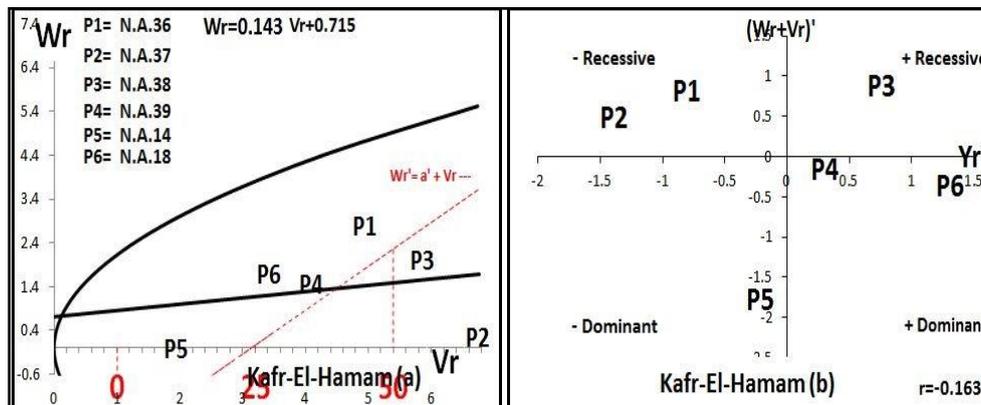


Fig. 15. Wr - Vr (a) and standardized deviations (b) graphs for seed oil content at Kafr-El-Hamam.

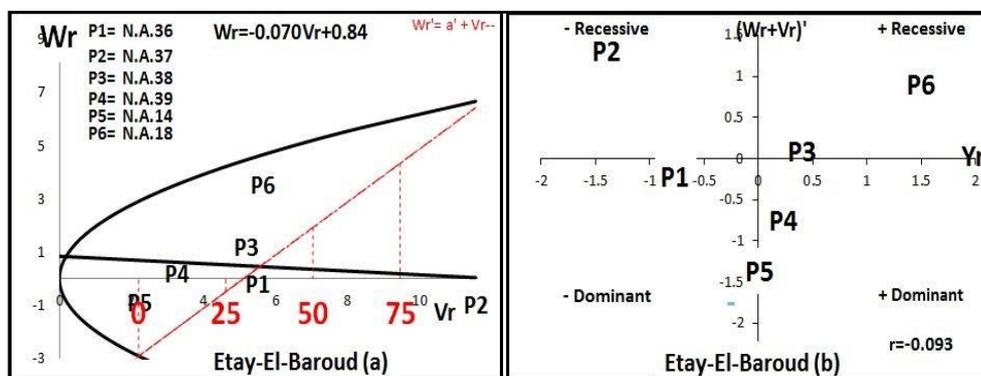


Fig. 16. Wr - Vr (a) and standardized deviations (b) graphs for seed oil content at Etay-El-Baroud.

CONCLUSION

In conclusion, the larger magnitude of dominance gene action compared with additive gene action for most studied traits at both locations, as they lesser the ratio of dominance average degree than unity. This was confirmed by estimating narrow-sense heritability, which was moderate to low for these traits. Hence, delayed selection in late generations would be effective at both locations for these traits. The GGE biplot revealed that

N.A.36 and N.A.39 at Kafr-El-Hamam and N.A.39 and N.A.14 at Etay-El-Baroud were the best general combiners for seed weight plant⁻¹ and N.A.36, N.A.38 and N.A.39 at Kafr-El-Hamam and N.A.36, N.A.39 and N.A.14 at Etay-El-Baroud for seed oil content, which associated with proportion of desirable genes either dominant or recessive. Superior heterotic effects than better parents for seed weight plant⁻¹ were observed in crosses [N.A.36 and N.A. 37] x [N.A.38 and N.A.14] at Kafr-El-Hamam and two crosses [N.A.37] x [N.A.38 and N.A.14] at Etay-El-Baroud as well as for seed oil content in four crosses [N.A.39 and N.A.14] x [N.A.37 and N.A.38] at Kafr-El-Hamam and two crosses in [N.A.18] x [N.A.37 and N.A.38] at Etay-El-Baroud.

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النظام الوراثي المتحكم في الصفات المحصولية في الكانولا

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لتحديد نوعي القدرة علي الائتلاف، قوة الهجين و السلوك الوراثي للصفات المحصولية، تم تهجين ٦ تركيب وراثية متباعدة من الكانولا باستخدام تصميم التزاوج النصف دائري (مع استبعاد الهجن العكسية). قيمت الاباء و هجنها باستخدام القطاعات الكاملة العشوائية في ثلاث مكررات بمحطة البحوث الزراعية بكفر الحمام/الشرقية و محطة البحوث الزراعية بايتاي البارود/البحيرة، مركز البحوث الزراعية، مصر. و اشارت نتائج متوسط درجة السيادة وكفاءة التوريث بالمعني الخاص الي أن الأرجحية و التغلب كان للفعل الجيني السادي لمعظم الصفات تحت الدراسة. و أشارت نتائج الشكل البياني للتراكيب الوراثية وتفاعلاتها مع البيئات (*GGE-biplot*) الي أن أفضل الاباء قدرة عامة علي الائتلاف كان *NA36* و *NA39* في كفر الحمام و *NA14* و *NA39* في ايتاي البارود لوزن البذور/نبات و *NA36* و *NA38* و *NA39* في كفر الحمام و *NA36* و *NA39* و *NA14* في ايتاي البارود لمحتوي الزيت بالبذور، و ذلك كان مصحوبا بنسبة من الجينات المرغوبة سواء كانت سائدة او متنحية. و اشارت النتائج الي ان الهجن الواعدة و المتفوقة عن أفضل الاباء كانت ؛ هجن *x [N.A.36 and N.A. 37]* و هجن *[N.A.38 and N.A.14]* في كفر الحمام و هجنين *[N.A.37] x [N.A.38]* في ايتاي البارود لوزن البذور/نبات، و ؛ هجن *[N.A.37 and N.A.38] x [N.A.39 and N.A.14]* في كفر كفر الحمام و هجنين *[N.A.18] x [N.A.37 and N.A.38]* في ايتاي البارود لمحتوي البذور من الزيت.

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