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Estimation of additive and epistatic gene effects for phenotypic and biochemical traits in double haploid lines of winter rapeseed (*Brassica napus* L.)

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Abstract

In this paper 60 doubled haploid lines of winter oilseed rape seed (*Brassica napus* L.) were studied. Genetic parameters as additive and epistatic effects were estimated for 24 traits. The results indicate the importance of both these effects for number of branches per plant, number of siliques per plant, linoleic acid, total of glucosinolates, total of alkenyl glucosinolates, gluconapin, glucobrassicanapin, progoitryn, napoleiferin and indolyl in both years of this study. Statistically significant epistatic effect and non-significant additive effect for thousand seed weight means that this trait was determined by genes with small individual effects but strong gene by gene interaction effects. Confounding epistatic effects in models suggested that inheritance of this trait is complex and polygenic.

Key words: Additive effect, doubled haploid lines, epistasis, oilseed rape

Introduction

The use of doubled haploids (DHs) in rapeseed (*Brassica napus* L.) breeding has many advantages. Production time of inbred lines for use as parents of hybrid cultivars is significantly reduced (Dias 2001; Cegielska-Taras et al. 2015). Another advantage of DH production is that there is only one round of recombination, which facilitates the tracking of parent's genes in next generation (Pink et al. 2008). The genetic homogeneity of DH lines allows to obtain more reliable data for quantitative traits in replicated trials. DH production is used widely by brassica scientists and breeders in phenotyping and genotyping studies (Chen et al. 2007; Radoev et al. 2008).

Complex traits, such as seed yield, oil content in seeds, and biochemical composition of seeds are usually controlled by multiple genetic factors each of which is regarded as a quantitative trait locus (QTL) (Badani et al. 2006; Chen et al. 2010). QTL analysis is a powerful tool for genetic investigation to identify loci responsible for the variation of phenotypic trait. The genetic complexity of quantitative traits and the interaction between genotype and environment make it difficult to screen for some genotypes from the progenies segregating for such traits. One approach to address this complexity is QTL mapping, which is used to identify significant genome regions associated with quantitative traits on a molecular linkage map (Basunanda et al. 2010; Li et al. 2014). Most studies of quantitative traits assume the additive effects of the loci that contribute to the expression of a trait (Bürger 2000). Gene effects interactions are commonly observed in artificial selection of traits (Hansen 2006). Epistasis means that the phenotypic effect of one gene is masked by a different gene (locus) and they are not additive in the contribution to a trait but depend on the genetic background (Wade et al. 2001). Epistasis is crucial in the understanding of the plants response to selection in breeding programs, and the genetic factors underlying complex traits.

Many research projects are aimed to improve the understanding of the inheritance of quantitative trait, which is a very complex issue because of the activity of multiple individual genes and interactions

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between them and environment. In purpose to estimate the parameters components for plants, several genetic statistical models have been developed. Gene action of quantitative traits can be evaluated by generation mean analysis, e.g. parental, F_1, F_2, BC_1. However, more effective estimation of additive and epistasis effects is on the basis of homozygous lines (Bocianowski 2012a, 2013, 2014; Bocianowski and Nowosad 2015; Kim et al. 2015; Monnahan and Kelly 2015; Ober et al. 2015). Therefore, the present study was aimed at the estimation of the additive and epistasis (additive-by-additive interaction) effects for doubled haploid lines population in oilseed rape.

Materials and methods

Plant material and experimentation

Plant material used in the paper includes 60 doubled haploid (DH) lines of winter oilseed rape developed from a single cross between recombinant inbred lines RIL 324/2 (high oleic acid content, 77.9%) as a female parent and RIL 622/3 (high oil content, 51.9% and high seed yield) as a male parent. DH lines were developed from F1 hybrids using isolated microspore cultures method, according to the procedure described by Cegielska-Taras et al. (2002) and Gacek et al. (2017).

Field experiment was conducted in Borowo (52°70'N, 16°46'E), Plant Breeding Strzelce Ltd., Co. – IHAR-PIB Group in two growing seasons, 2014-2015 and 2015-2016 in a randomized blocks design (RBD) with three replications. Each plot contained four rows two meters long. Distance between rows was 30 cm. The field management followed standard agricultural practice.

Yield related and biochemical traits evaluated in the field were: beginning of flowering (days), length of flowering (days), plant height (cm), number of branches per plant (no.), number of siliques per plant, silique length (mm), number of seeds per silique, thousand seed weight (g). DH lines were also studied for observed by biochemical traits of seeds namely, oil content (%), oleic acid (%), linoleic acid (%), linolenic acid (%), palmitic acid (%), stearic acid (%), eicosenoic acid (%), erucic acid (%), total of glucosinolates (µM/g of seeds), total of alkenyl glucosinolates (µM/g of seeds), gluconapin (µM/g of seeds), glucobrassicanapin (µM/g of seeds), progoitryn (µM/g of seeds), napoleiferin (µM/g of seeds), indolyl (µM/g of seeds) and 4-hydroksyglucobrassin (µM/g of seeds).

The beginning of flowering was measured as a number of days since the beginning of January unto the beginning of the flowering. Length of flowering was the number of days from the beginning to the end of flowering. Plant height was measured on three randomly selected plants from each plot after the end of flowering time. Number of branches per plant and siliques per plant were recorded on three well-developed, randomly selected plants from each plot, at the green siliques stage. Silique length and number of seeds per silique were recorded on 25 siliques from each plot. Siliques were collected at the stage of mature seeds from the main branch and then dried. Thousand seed weight was recorded from the average of three measurements from the mixed seeds of all plants in a plot. Seed yield per plot was also measured. Oil contents were measured by nuclear magnetic resonance (NMR) spectroscopy. The fatty acid composition and glucosinolate contents in seeds was performed with gas chromatography analyses.

Statistical analyses

The normality of distribution of the traits was tested using Shapiro-Wilk's normality test and having normally distributed traits, it was assumed that the data followed the multivariate normal distribution. The two-way (fixed effects) analysis of variance (ANOVA) was carried out to determine the effects of DH lines, years and DH lines x years interaction on the variability of observed traits. The relationships between observed traits was estimated using Pearson correlation coefficients on the basis of means of lines. The correlation coefficients between means of lines in both years for each trait were also estimated and tested by *t*-test.

Estimation of the additive gene effects and epistasis (additive-by-additive interaction of homozygous loci) effects on the basis of phenotypic and biochemical observations require identification of groups of extreme DH lines, i.e. lines with the minimal and maximal expression of the observed trait (Choo and Reinbergs 1982). The group of minimal (maximal) lines consists of the lines which contain, theoretically, only alleles reducing (increasing) the value of the trait. The groups of extreme lines were identified by the quantile method (Bocianowski et al. 1999), in which the lines with the mean values, bigger (smaller) than 0.97 (0.03) quantile of the empirical distribution of means are assumed as maximal (minimal) lines. The choose the quantiles 0.97 and 0.03 is results of previously study (Bocianowski et al. 1999). The total additive effect (*a*) of all genes controlling the trait and

the total epistasis effect (*aa*) may be estimated by the formulas (Bocianowski and Krajewski 2009; Bocianowski 2012b):

$$\hat{a} = \frac{1}{2}\left(\overline{L}_{\max} - \overline{L}_{\min}\right) \quad (1)$$

and

$$\hat{aa} = \frac{1}{2}\left(\overline{L}_{\max} + \overline{L}_{\min}\right) - \overline{L}, \quad (2)$$

where $\overline{L}_{\max}$ and $\overline{L}_{\min}$ denote the means for the groups of maximal and minimal DH lines, respectively, $\overline{L}$ denotes the mean value for all DH lines. The test statistics to verified hypotheses about genetic parameters different than zero are given by

$$F_a = \frac{MS_a}{MS_e} \text{ and } F_{aa} = \frac{MS_{aa}}{MS_e},$$

where MS_a denote mean square for *a*, MS_{aa} – mean square for epistasis, MS_e – mean square for residual.

Results and discussion

All the 24 observed traits have a normal distribution. Results of ANOVA indicates that the main effects of DH lines were significant (P<0.001) for all the traits under study. The main effects of years were statistically significant for all the traits except, length of flowering, number of siliques per plant, linoleic acid and total of alkenyl glucosinolates. The DH lines × years interaction effects were significant for all the traits studied (Table 1). The effects of genetic parameters were estimated for years separately as well as for average of years. Results were partially

Table 1. Mean squares from two-way analysis of variance for observed traits

Source of variation	DH lines	Years	DH lines x years	Residual
Degrees of freedom	59.00	1.00	59.00	240
Beginning of flowering (days)	165.325***	646.397***	69.105***	0.963
Length of flowering (days)	82.516***	0.003	84.812***	2.672
Plant height (cm)	7035.84***	526.47*	1456.98***	84.61
Number of branches per plant	173.749***	81.435***	97.485***	6.211
Number of siliques per plant	1047885.000***	154557.00	734006.00***	49429
Silique length (mm)	1667.490***	112923.360***	425.460***	65.39
Number of seeds per silique	359.090***	442.040***	283.180***	31.99
Thousand seed weight (g)	7.412***	1213.729***	6.577***	0.169
Oil content (%)	11.775***	899.684***	5.880***	1.595
Oleic acid (%)	108.365***	78.307***	2.105***	0.945
Linoleic acid (%)	78.014***	0.455	1.098***	0.54
Linolenic acid (%)	4.331***	112.896***	0.286***	0.117
Palmitic acid (%)	0.437***	4.160***	0.027***	0.01
Stearic acid (%)	0.375***	0.173**	0.054***	0.021
Eicosenoic acid (%)	0.052***	0.047**	0.011**	0.006
Erucic acid (%)	0.013***	0.034*	0.013***	0.006
Total of glucosinolates (µM/g of seeds)	33.006***	16.857***	1.713**	1.041
Total of alkenyl glucosinolates (µM/g of seeds)	20.245***	0.245	1.575***	0.823
Gluconapin (µM/g of seeds)	1.067***	0.642***	0.118***	0.056
Glucobrassicanapin (µM/g of seeds)	0.179***	0.521***	0.020***	0.006
Progoitryn (µM/g of seeds)	9.590***	2.010*	0.724***	0.384
Napoleiferin (µM/g of seeds)	0.028***	0.056***	0.003***	0.001
Indolyl (µM/g of seeds)	0.452***	0.841***	0.159***	0.013
4-hydroksyglucobrassin (µM/g of seeds)	5.638***	12.844***	0.489***	0.185

* P<0.05; ** P<0.01; *** P<0.001

Table 2. The correlation matrix for the traits studied for 2015 (above diagonal) and 2016 (below diagonal)

Trait(tr)	tr1	tr2	tr3	tr4	tr5	tr6	tr7	tr8	tr9	tr10	tr11	tr12	tr13	tr14	tr15	tr16	tr17	tr18	tr19	tr20	tr21	tr22	tr23	tr24
tr1	**1.00**	-0.23	0.42	0.26	0.20	0.33	0.19	-0.15	0.20	-0.11	0.15	-0.09	0.11	0.11	-0.31	-0.13	-0.11	-0.07	-0.16	-0.16	-0.03	0.01	0.19	-0.21
tr2	-1.00	**1.00**	0.06	-0.05	0.09	-0.15	-0.07	-0.05	0.13	-0.01	-0.01	0.04	0.10	-0.01	0.16	0.04	0.02	-0.03	-0.08	0.02	-0.01	0.03	-0.05	0.13
tr3	0.33	-0.33	**1.00**	0.07	0.08	0.22	0.05	0.24	0.38	0.08	-0.08	0.00	-0.09	-0.15	-0.14	0.07	-0.19	-0.16	-0.13	-0.03	-0.20	-0.03	-0.12	-0.11
tr4	0.45	-0.45	0.00	**1.00**	0.69	0.12	-0.01	-0.19	0.34	0.04	-0.01	-0.05	-0.08	-0.05	-0.18	-0.17	-0.19	-0.17	-0.14	-0.24	-0.17	-0.17	0.00	-0.14
tr5	0.45	-0.45	0.03	0.73	**1.00**	0.19	-0.10	-0.24	0.20	-0.06	0.06	0.06	-0.03	0.06	-0.12	-0.08	-0.23	-0.24	-0.15	-0.29	-0.25	-0.32	0.05	-0.12
tr6	0.12	-0.12	0.08	0.08	0.03	**1.00**	0.34	-0.09	0.41	-0.05	0.04	0.19	0.06	-0.36	-0.17	-0.01	-0.14	-0.10	-0.09	-0.29	-0.08	-0.12	-0.14	-0.10
tr7	-0.16	0.16	0.20	-0.18	-0.29	0.53	**1.00**	-0.16	0.10	-0.01	0.01	0.08	-0.01	-0.21	-0.23	-0.01	0.14	0.13	0.10	0.02	0.14	0.18	0.00	0.10
tr8	-0.17	0.17	0.17	-0.38	-0.25	-0.44	-0.26	**1.00**	0.12	-0.04	0.03	0.19	0.00	-0.43	0.07	0.12	0.06	0.06	0.10	0.13	0.02	0.16	-0.19	0.11
tr9	-0.01	0.01	-0.14	0.23	0.19	0.33	0.09	-0.15	**1.00**	-0.05	0.03	0.23	-0.03	-0.50	-0.03	0.27	-0.41	-0.45	-0.32	-0.52	-0.46	-0.36	-0.24	-0.09
tr10	0.02	-0.02	0.08	-0.04	-0.06	-0.21	-0.07	0.34	-0.26	**1.00**	-0.99	-0.67	-0.66	-0.05	0.42	-0.19	-0.24	-0.22	-0.18	-0.03	-0.24	-0.17	-0.10	-0.14
tr11	-0.02	0.02	-0.04	0.05	0.08	0.21	0.06	-0.30	0.29	-0.99	**1.00**	0.56	0.61	0.06	-0.45	0.16	0.26	0.25	0.20	0.06	0.28	0.19	0.10	0.12
tr12	-0.03	0.03	-0.24	0.01	-0.05	0.25	0.16	-0.44	0.24	-0.68	0.58	**1.00**	0.39	-0.31	-0.24	0.14	0.11	0.08	0.13	-0.09	0.08	0.11	-0.04	0.12
tr13	0.05	-0.05	0.00	0.01	0.09	0.02	-0.03	-0.24	0.01	-0.67	0.63	0.38	**1.00**	0.14	-0.33	0.12	0.06	0.04	-0.02	-0.07	0.07	0.06	0.01	0.07
tr14	0.02	-0.02	0.20	-0.12	0.04	-0.43	-0.36	0.39	-0.43	0.23	-0.19	-0.56	-0.02	**1.00**	-0.14	-0.22	0.01	-0.11	-0.19	0.07	-0.08	-0.13	0.32	0.13
tr15	-0.15	0.15	-0.25	-0.27	-0.25	-0.18	-0.08	0.20	-0.29	0.63	-0.66	-0.33	-0.44	0.01	**1.00**	0.41	-0.06	-0.10	-0.03	-0.02	-0.12	-0.17	0.08	0.01
tr16	0.12	0.03	0.01	0.04	0.11	0.07	0.03	0.09	-0.01	0.04	-0.10	0.17	0.16	0.10	0.00	**1.00**	-0.22	-0.19	-0.21	-0.18	-0.17	-0.14	-0.07	-0.17
tr17	-0.32	0.32	-0.10	-0.02	-0.10	0.04	0.05	-0.04	0.06	-0.26	0.27	0.13	0.10	-0.17	-0.08	0.04	**1.00**	0.90	0.87	0.75	0.87	0.71	0.43	0.63
tr18	-0.28	0.28	-0.14	0.04	-0.10	0.08	0.20	-0.17	0.06	-0.31	0.31	0.20	0.12	-0.36	-0.11	-0.01	0.85	**1.00**	0.90	0.84	0.99	0.87	0.19	0.25
tr19	-0.35	0.35	-0.21	-0.08	-0.21	0.04	0.19	-0.13	-0.10	-0.26	0.26	0.18	0.09	-0.30	0.05	0.00	0.76	0.91	**1.00**	0.73	0.83	0.67	0.20	0.35
tr20	-0.30	0.30	-0.11	-0.04	-0.13	-0.13	0.14	0.09	-0.05	-0.11	0.12	0.03	-0.03	-0.15	-0.02	0.19	0.75	0.85	0.77	**1.00**	0.79	0.86	0.08	0.22
tr21	-0.24	0.24	-0.11	0.09	-0.06	0.11	0.19	-0.20	0.10	-0.33	0.34	0.20	0.14	-0.38	-0.15	-0.06	0.84	0.99	0.86	0.81	**1.00**	0.87	0.20	0.20
tr22	-0.36	0.36	-0.17	-0.07	-0.16	0.02	0.26	-0.17	0.19	-0.20	0.18	0.31	-0.09	-0.37	-0.05	-0.01	0.65	0.76	0.66	0.79	0.73	**1.00**	0.05	0.06
tr23	-0.32	0.32	0.06	-0.13	-0.12	0.05	0.01	0.10	-0.10	0.03	-0.02	-0.15	0.02	0.32	0.04	-0.02	0.30	-0.04	-0.01	0.02	-0.05	-0.07	**1.00**	0.40
tr24	-0.09	0.09	0.01	-0.07	0.02	-0.08	-0.27	0.18	0.06	-0.05	0.06	0.00	0.02	0.15	-0.02	-0.17	0.59	0.10	0.07	0.13	0.09	0.08	0.40	**1.00**

Yellow cells - statistical significant correlation coefficients, $p<0.05$

tr1 = Beginning of flowering, tr2 = Length of flowering, tr3 = Plant height, tr4 = No. of branches per plant, tr5 = No. of siliques per plant, tr6 = Silique length, tr7 = No. of seeds/silique, tr8 = Thousand seed weight, tr9 = Oil content, tr10 = Oleic acid, tr11 = Linoleic acid, tr12 = Linolenic acid, tr13 = Palmitic acid, tr14 = Stearic acid, tr15 = Eicosenoic acid, tr16 = Erucic acid, tr17 = Total of glucosinolates, tr18 = Total of alkenyl glucosinolates, tr19 = Gluconapin, tr20 = Glucobrassicanapin, tr21 = Progoitryn, tr22 = Napoleiferin, tr23 = Indolyl, tr24 = 4-Hydroksyglucobrassin

Table 3. Estimates of additive and epistasis effects for observed traits of doubled haploid lines and correlation coefficients (*r*) between means of lines in both years

Traits	Year	Estimates of		Mean value	*r*
		additive effect, *a*	epistatic effect, *aa*		
Beginning of flowering (days)	2015	4.000$^{\#}$	1.533	117.467	0.426***
	2016	8.250	-1.400	118.650	
		5.625	**-0.433**	**118.058**	
Length of flowering (days)	2015	2.750*$^{\#}$	0.400	24.350	-0.020
	2016	8.250**	1.400*	24.350	
		4.375*	**0.775**	**24.350**	
Plant height (cm)	2015	18.350*$^{\#}$	-0.450	146.850	0.658***
	2016	14.800*	-1.823	147.373	
		15.150*	**-1.187**	**147.112**	
No. of branches per plant (no.)	2015	3.500**$^{\#}$	0.552**	10.168	0.281
	2016	3.193**	1.072**	9.955	
		2.348*	**0.173**	**10.062**	
No. of siliques per plant (no.)	2015	197.950***$^{\#}$	29.157**	434.843	0.191
	2016	372.050***	123.857***	444.543	
		236.675***	**49.982****	**439.693**	
Silique length (mm)	2015	14.858**$^{\#}$	3.204**	59.293	0.656***
	2016	8.658*	0.370	51.372	
		10.539*	**2.906***	**55.333**	
No. of seeds per silique (no.)	2015	4.860**$^{\#}$	0.797**	14.803	0.120
	2016	6.688**	0.064	15.298	
		4.411**	**0.798***	**15.051**	
Thousand seed weight (g)	2015	0.525$^{\#}$	0.108*	5.278	0.070
	2016	0.864*	-0.139	4.453	
		0.526*	**-0.028**	**4.865**	
Oil content (%)	2015	3.668$^{\#}$	0.438	43.275	0.339**
	2016	3.678	0.119	40.114	
		3.054	**-0.053**	**41.694**	
Oleic acid (%)	2015	7.420*	1.736	66.914	0.964***
	2016	6.673	1.446	67.847	
		6.875*	**1.702**	**67.380**	
Linoleic acid (%)	2015	5.898**	-1.602**	15.485	0.974***
	2016	5.585**	-1.329*	15.414	
		5.663**	**-1.387***	**15.450**	
Linolenic acid (%)	2015	1.642*	0.067	9.858	0.879***
	2016	1.792*	0.204	8.738	
		1.637*	**0.056**	**9.298**	
Palmitic acid (%)	2015	0.550*	-0.021	4.305	0.889***
	2016	0.500*	-0.019	4.519	
		0.508*	**-0.020**	**4.412**	
Stearic acid (%)	2015	0.450*	0.032	2.085	0.787***
	2016	0.667**	-0.079	2.129	
		0.496*	**-0.011**	**2.107**	
Eicosenoic acid (%)	2015	0.208*	0.034	1.342	0.658***
	2016	0.200*	0.048	1.319	
		0.162*	**0.016**	**1.330**	

Erucic acid (%)	2015	0.233***	0.214***	0.019	0.973***
	2016	0.000	0.000	0.000	
		0.117* **	**0.107*** **	**0.010**	
Total of glucosinolates (μM/g of seeds)	2015	6.250***	1.457**	9.293	0.918***
	2016	5.117***	1.424**	9.726	
		5.663* **	**1.462** **	**9.509**	
Total of alkenyl glucosinolates (μM/g of seeds)	2015	4.842***	2.036***	4.789	0.865***
	2016	4.308***	2.189***	4.737	
		4.575* **	**2.112*** **	**4.763**	
Gluconapin (μM/g of seeds)	2015	1.167***	0.377***	1.390	0.820***
	2016	0.875***	0.319**	1.306	
		1.021* **	**0.348*** **	**1.348**	
Glucobrassicanapin (μM/g of seeds)	2015	0.500***	0.181***	0.319	0.856***
	2016	0.358***	0.148***	0.243	
		0.429* **	**0.164*** **	**0.281**	
Progoitryn (μM/g of seeds)	2015	3.142***	1.411***	3.014	0.865***
	2016	3.025***	1.562***	3.163	
		3.067* **	**1.503*** **	**3.089**	
Napoleiferin (μM/g of seeds)	2015	0.158***	0.109***	0.049	0.817***
	2016	0.150***	0.126***	0.024	
		0.154* **	**0.118*** **	**0.036**	
Indolyl (μM/g of seeds)	2015	0.767***	0.581***	0.186	0.479***
	2016	0.700***	0.418***	0.282	
		0.658* **	**0.433*** **	**0.234**	
4-hydroksyglucobrassin (μM/g of seeds)	2015	2.117**	-0.297*	4.314	0.842***
	2016	2.142**	0.000	4.692	
		2.100 **	**-0.178**	**4.503**	

* P<0.05; ** P<0.01; *** P<0.001; The estimated values of additive and epistatic effects are given in bold figure (average over two years)
#Results partially presented for nine phenotypic traits in first growing season (2014/15) (Bocianowski et al. 2017).

presented for nine phenotypic traits in first growing season (2014/15) (Bocianowski et al. 2017). Table 2 presents a correlation matrix for the observed traits. Thirty pairs of traits were positively correlated in both the years of study however, for eight pairs significant negative correlation coefficients were recorded (Table 2). Only for one pair of traits – thousand seed weight and stearic acid – we obtained correlation coefficients with opposite sign in different years of the study (-0.43 in 2015 and 0.39 in 2016 were recorded). Quality traits were positively correlated. These results are characteristic for DH lines population. Many important traits are negatively or positively correlated, because they may be controlled by a few or similar genes or they may be developmentally or structurally related (Bocianowski 2012b) in certain aspects.

Estimates of additive gene action effects based on DH lines were significantly larger than zero in both years of the study for the length of flowering, plant height, number of branches per plant, number of siliques per plant, silique length, number of seeds per silique, linoleic acid, palmitic acid, stearic acid, eicosenoic acid, total of glucosinolates, total of alkenyl glucosinolates, gluconapin, glucobrassicanapin, progoitryn, napoleiferin, indolyl and 4-hydroksyglucobrassin. In only first year of the study, the additive gene action effect was significant for oleic acid and erucic acid however, in 2016 the additive gene action was observed for thousand seed weight (Table 3). Estimates of epistasis effects were statistically significant in both the years of study for number of branches per plant, number of siliques per plant, linoleic acid (negative effects' values), total of glucosinolates, total of alkenyl glucosinolates, gluconapin, glucobrassicanapin, progoitryn, napoleiferin and indolyl (Table 3). However, during 2015, epistasis effects were significant for silique length, number of seeds per silique and erucic acid but these effects were significant for length of flowering and 4-hydroksyglucobrassin (Table 3) in 2016. Different statistical significances of additive and epistatic effects in particular years of study

were perhaps due to different expression of genes which determined the traits in the years, 2015 and 2016.

Estimation of genetic parameters plays an important role in rapeseed breeding. The present findings indicated the importance of both additive and epistatic gene effects for number of branches per plant, number of siliques per plant, linoleic acid, total of glucosinolates, total of alkenyl glucosinolates, gluconapin, glucobrassicanapin, progoitryn, napoleiferin and indolyl in both years of this study. The presence of epistasis has important implication for any breeding program since it has been reported for many traits in a number of crops such as barley (Bocianowski et al. 2016), maize (Li et al. 2016), rice (Matsubara et al. 2015), and wheat (Jaiswal et al. 2016). Several studies conducted on quantitative genetics implied that epistatic interactions among different loci often have considerable effects on adaptability and affect the phenotype (Pérez de la Vega et al. 1994). Luo et al. (2017) conducted genome-wide association study for eight yield-related traits to define the additive, dominance, epistasis effects, and their environment interaction. They observed that non-additive effects had great influence on heritability and epistasis and also noted the importance of environmental interactions. Liu et al. (2017) studied the significance of additive, dominance, and epistatic effects for determining hybrid seed yield in a biparental rapeseed population. Their study revealed that the heterosis performance in rapeseed hybrids was driven by all these effects. Statistically significant epistasis effect and non-significant additive effect for thousand seed weight means that this trait was probably determined by genes with small individual effects but strong gene-by-gene interaction effects (Bocianowski et al. 2017). Confounding epistasis effects in models suggested that inheritance of this trait is complex and polygenic (Krajewski et al. 2012).

Author's contribution

Conceptualization of research (JB, KN); Designing of the experiments (AD, JW); Contribution of experimental materials (AD, JW); Execution of field/lab experiments and data collection (AD, JW); Analysis of data and interpretation (JB, KN); Preparation of the manuscript (JB, KN, AD, JW).

Declaration

The authors declare no conflict of interest.

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