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Study of gene effects for seed oil yield and its component traits in *bidi* tobacco (*Nicotiana tabacum* L.)

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Abstract
Tobacco is one of the important non-food crops traditionally used for manufacturing of cigarettes, it is also considered as an oilseed crop as the tiny tobacco seeds contain 30 to 40 percent oil. There is little information on gene effects governing seed oil yield in tobacco available. Hence present study on genetic analysis for seed oil yield and its components were carried out in *bidi* tobacco using six basic generations *viz*., P_1, P_2, F_1, F_2, BC_1 and BC_2 of five different crosses namely, I) Dediapada Selection x A 145, II) Dediapada Selection x A 119, III) GABT 11 x Dediapada Selection, IV) Jayalakshami x Sanand Local and V) A 119 x L 108-15-3. Three parameters model was found adequate in cross I for branches per plant, for test weight in crosses II and III, and for seed weight per capsule in cross V. All types of gene effects i.e., additive (*d*), dominant (*h*), additive x additive (*i*), additive x dominant (*j*) and dominant x dominant (*l*) were significant in most traits studied in all these crosses. Additive gene effect was found prominent for test weight and seed oil content in cross I, for leaf yield per plant in cross II, for days to capsule maturity in crosses III and IV, and for branches per plant, test weight, leaf yield per plant and seed oil yield per plant in cross V. Thus, the magnitude and type of gene effects differed for different characters in the same cross and for the same character in different crosses, which requires specific handling of individual crosses in segregating generations for further improvement.

Keywords: *Bidi* tobacco, *Nicotiana tabacum*, seed oil yield, gene effects, generation mean ananlysis

1. Introduction
Tobacco (*Nicotiana tabacum* L.) is one of the most widely cultivated non-food crops worldwide and is grown in about 120 countries. It belongs to the *Nicotiana* genus, which is named after Jean Nicot de Villemain who, in 1560, became the first person to import these plants from the Americas to Europe. Most tobacco varieties cultivated today belong to the species of *N. tabacum* and more than 1600 varieties of *N. tabacum* are listed in the National Plant Germplasm System (Sierro *et. al.*, 2014) [18]. Over 75 naturally occurring species of tobacco have been classified by Goodspeed and Knapp (Sierro *et. al.*, 2014) [18], only two species *viz*; *N. tabacum* and *N. rustica* are economically important. Farmers in India predominantly grow these species for commercial cultivation. The species, N. tabacum (2n=4x=48) has evolved through the interspecific hybridization of the ancestors of *N. sylvestris* (2n=24, maternal donor) and *N. tomentosiformis* (2n=24, paternal donor) about 0.2 million years ago (Leitch *et al.*, 2008) [7]. Tobacco is a complex allotetraploid with genome size of 4.5 Gb with significant proportion (> 70%) of repeats (Zimmerman and Goldberg, 1977; Renny-Byfield *et al.*, 2011) [19, 16].
The tiny tobacco seed contains 30 to 40 percent oil and linoleic acid is the major constitutes fatty acid (66 – 76%). Another important feature of tobacco seed oil is that it contains high PUFA value and 1.5 per cent (Ω)-3-fatty acid which is an essential fatty acid for human body. Chemical quality of the tobacco seed oil is comparable to safflower oil and is superior to groundnut oil. With increasing importance for research on non-conventional uses of tobacco, a critical examination of the potential of tobacco as 'an oil seed crop' was taken up with very encouraging results. The refined tobacco seed oil has already been in use as edible oil in countries like Bulgaria, Turkey, Tunisia and Greece (Sarala *et al.*, 2013) [17].
Various biometrical techniques are extensively used for estimation of relative magnitude of different components of genetic variation.

One of the methods for estimation of genetic parameters is generation mean analysis, in which epistatic effects could also be estimated. Six basic generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) can give accurate information in relating average dominance ratio and its inheritance (Mather and Jinks, 1982; Kearsy and Pooni, 1996) [8]. The present investigation, therefore, taken up using generation mean analysis involving six generations of five crosses of seven diverse genotypes/cultivars of tobacco to estimate the nature and magnitude of gene action governing seed oil yield and its components in *bidi* tobacco.

2. Materials and Methods

2.1 Study area

The present investigation on Genetic analysis for Seed oil yield and its components in *bidi* tobacco (*Nicotiana tabacum* L.) was conducted at Bidi Tobacco Research Station, Anand Agricultural University, Anand, Gujarat during *kharif-rabi* 2016-17.

2.2 Experimental Material

The experimental material comprised of seven parental lines *viz*; Dediapada Selection, A 119, A 145, GABT 11, Sanand Local, Jayalakshami and L 108-15-3 were selected based on their geographic origin and wide variation in morphological characters. Six generations (P_1, P_2, F_1, F_2, BC_1 and BC_2) of five families *viz*., I) Dediapada Selection x A 145, II) Dediapada Selection x A 119, III) GABT 11 x Dediapada Selection, IV) Jayalakshami x Sanand Local and V) A 119 x L 108-15-3 were grown in Compact Family Block Design with four replications. Each plot had one row each for parents and F_1, two rows for each of B_1 and B_2 and four rows for F_2 population. Each row was accommodated ten plants with inter- and intra-row spacing of 90 and 75 cm, respectively.

2.3 Observations recorded

The characters studied in this experiment were Days to flowering, Plant height, Leaves per plant, Branches per plant, Capsules per plant, Days to capsule maturity, Capsule weight (mg), Seed weight per capsule (mg), Test weight (mg), Leaf yield per plant (g), Seed yield per plant (g), Seed oil percent (%) and Seed oil yield per plant (g). The observations for all the matriculate characters under study were recorded in each experiment unit i.e., generation as five plants each in P_1, P_2 and F_1, ten plants each in B_1 and B_2 and twenty plants in F_2. The five competitive plants were selected randomly for recording observations of respective traits.

2.4 Statistical analysis

The mean data of six generations *viz.*, P_1, P_2, F_1, F_2, BC_1 and BC_2 were subjected to joint scaling test to detect gene effects and to test adequacy of 3 parameter model and six parameter models including non-allelic interaction (Cavalli, 1952) [1]. The adequacy of dominance-additive model was determined by employing simple scaling test A, B, C and D as suggested by Mather and Jinks (1971) [9]. The additive-dominance was considered adequate when all the individual scaling test were found non-significant.

3. Results

The choice of breeding procedures for genetic improvement of any crop is largely depend upon the knowledge of the type and relative amount of genetic component and the presence of non-allelic interactions of different characters (Ninghot *et al.*, 2016) [10]. Mean of six generations *viz.*, P_1, P_2, F_1, F_2, BC_1 and BC_2 of each cross are presented in Table 1 and the results of scaling test and genetic parameters in each cross (Table 2) are discussed character wise, hereunder.

3.1 Scaling test

The significant value of joint scaling test χ^2 suggested six parameter model was adequate for all the traits in these five crosses, except branches per plant in cross I, seed weight per capsule in cross V and test weight in crosses II and III. The estimate of gene effects revealed that mean effects (*m*) were significant for all the traits in all these crosses barring cross IV for capsules per plant.

3.2 Genetic parameters

The principle gene effects i.e., mid-parental effect (*m*), additive (*d*) and dominance (*h*) as well as interaction effects additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) were computed using six parameter model of generation mean analysis in a character cross combination where either of four or all simple scaling tests i.e. A, B, C, and D were significant.

4. Discussion

4.1 Days to flowering

The estimates of gene effects for days to flowering indicated involvement of both, additive and non-additive gene effects in crosses I, III and IV. The type of gene action responsible for the inheritance of the trait revealed that homozygous elite recombinants could be developed by following *inter se* crossing of desirable segregants. These findings agree with the results of Dave (2012) [2], Hadiya *et al.* (2017) [3] and Katba *et al.* (2019) [4]. The pedigree method of breeding could be profitably use in crosses II and V as additive gene action was found to play a major role due to its higher magnitude. Similar results were reported by Rawool (2012) [15] and Kuchhadiya (2014) [6].

4.2 Leaves per plant

Both additive and non-additive gene effects were found significant in crosses I, III and V; whereas preponderance of additive type of gene action was observed in crosses II and IV. Hence, conventional approach of pedigree method in cross II and IV, and population improvement approaches like recurrent selection and biparental mating shall be remunerative in rest crosses for improving number of leaves. The opposite signs of the components (h) and (l) showed the duplicate type of epistasis in all the crosses. Hadiya *et al.* (2017) [3] noticed additive and non-additive effects while Kuchhadiya (2014) [6] observed additive gene effect in expression of this trait.

Table 1: Mean and standard error of various generations involved in generation mean analysis

Cross	Generations					
	P_1	**P_2**	**F_1**	**F_2**	**BC_1**	**BC_2**
Days to flowering						
I	43.45±0.85	65.10±1.22	60.20±0.67	53.48±0.66	48.40±0.73	53.28±0.83
II	42.80±0.91	54.55±0.46	50.10±0.76	52.31±0.62	46.58±0.98	55.35±0.55
III	111.55±1.28	43.50±0.55	51.45±0.64	59.93±1.06	83.45±1.57	48.38±1.04

IV	74.40±0.76	52.15±0.59	64.40±0.93	70.64±1.35	64.35±1.08	54.13±1.20
V	56.80±0.69	64.85±0.57	61.95±0.78	63.74±0.58	62.40±0.78	63.53±0.70
Leaves per plant						
I	11.15±0.21	17.75±0.25	14.75±0.14	14.65±0.16	15.58±0.17	16.50±0.25
II	11.40±0.32	14.70±0.27	15.80±0.33	14.90±0.22	14.05±0.23	14.75±0.27
III	36.55±0.79	10.90±0.33	18.25±0.47	16.76±0.25	18.00±0.36	14.95±0.26
IV	21.10±0.27	17.40±0.19	18.90±0.27	17.83±0.22	17.90±0.29	18.73±0.23
V	14.30±0.30	15.10±0.22	17.10±0.31	16.01±0.18	17.23±0.24	16.23±0.25
Plant height (cm)						
I	51.25±1.96	100.75±1.36	80.05±1.94	82.64±1.96	78.03±2.70	89.98±2.07
II	53.05±1.47	130.45±1.17	100.75±1.67	104.03±1.61	79.83±1.13	126.25±2.28
III	143.90±2.03	53.55±1.82	89.00±1.79	85.54±1.93	113.85±4.05	72.45±1.39
IV	141.55±2.93	73.45±2.33	94.10±2.06	90.21±2.16	108.18±2.94	77.75±1.70
V	132.90±0.81	111.45±1.46	130.90±1.69	133.85±1.21	131.48±2.70	113.75±1.43
Branches per plant						
I	4.85±0.20	6.30±0.16	5.75±0.14	5.53±0.10	5.30±0.13	6.43±0.15
II	4.75±0.14	9.95±0.29	8.85±0.15	8.45±0.15	5.85±0.18	9.55±0.16
III	9.55±0.22	4.50±0.18	7.05±0.18	7.75±0.13	9.78±0.13	5.58±0.17
IV	7.70±0.21	7.15±0.17	9.25±0.14	9.36±0.13	8.45±0.15	8.75±0.15
V	10.20±0.20	8.85±0.21	11.05±0.26	9.21±0.17	9.75±0.20	9.70±0.21
Capsules per plant						
I	238.95±5.11	540.55±15.37	482.40±9.06	468.85±9.62	388.33±13.66	403.48±10.86
II	194.40±10.88	482.80±11.56	664.00±13.73	404.75±10.08	381.08±13.07	354.88±13.11
III	247.85±12.76	200.45±5.66	684.10±18.70	459.05±13.06	395.65±19.29	266.30±18.92
IV	199.45±6.95	382.30±12.91	606.20±11.34	360.94±11.01	397.90±14.67	470.55±15.50
V	468.55±12.15	544.00±15.69	514.20±17.59	413.76±12.71	457.28±15.06	489.20±16.00
Days to capsule maturity						
I	78.35±0.79	115.35±1.05	110.30±0.80	103.49±0.74	98.40±1.28	103.28±0.98
II	74.25±0.96	130.20±0.54	116.70±1.35	124.98±0.96	121.58±0.98	130.35±0.55
III	170.85±1.70	74.05±1.07	76.45±0.64	134.93±1.06	151.35±1.60	123.38±1.04
IV	119.65±1.55	97.15±0.60	88.80±1.39	100.85±0.78	114.35±1.21	91.13±0.93
V	131.80±0.68	114.85±0.57	107.30±0.69	110.74±0.63	122.40±0.87	115.53±0.80
Capsule weight (mg)						
I	256.90±5.22	271.78±5.50	332.61±8.03	311.54±4.56	318.74±6.94	317.28±5.66
II	253.33±3.20	339.36±3.13	327.43±2.92	369.72±3.40	325.80±5.96	324.66±4.66
III	301.21±6.58	253.98±4.96	331.37±9.69	298.29±6.24	293.73±8.68	334.40±9.23
IV	345.42±6.40	262.01±6.48	339.31±7.37	299.71±4.96	319.43±7.20	337.46±6.05
V	315.37±6.35	390.02±12.13	343.01±6.81	322.98±5.11	326.05±7.10	314.49±8.35
Seed weight per capsule (mg)						
I	147.54±1.40	139.55±2.14	206.82±3.92	209.38±3.11	232.68±4.55	231.61±4.74
II	146.93±3.20	247.13±3.13	239.02±2.92	269.89±3.40	237.83±5.96	237.00±4.66
III	219.88±4.81	145.41±3.62	241.90±7.07	217.75±4.22	214.42±5.92	244.11±6.06
IV	232.16±4.67	153.27±4.73	247.70±5.38	218.79±3.48	233.18±4.40	246.35±4.84
V	230.22±4.64	249.72±8.86	250.40±4.97	235.77±3.73	238.02±5.18	229.58±6.09
Test weight (mg)						
I	59.02±0.92	68.38±1.05	67.48±0.89	56.48±0.71	57.32±1.08	62.13±0.77
II	59.75±1.00	60.61±0.80	67.76±1.10	62.77±1.09	66.13±1.30	62.34±1.10
III	58.09±1.30	59.51±1.04	71.87±0.76	62.42±1.36	61.43±1.28	66.43±1.45
IV	46.98±1.12	65.23±0.83	53.46±1.35	47.08±0.76	50.66±1.10	57.86±0.82
V	58.64±1.13	68.43±1.15	65.59±1.03	60.87±0.61	59.80±0.75	68.81±0.93
Leaf yield per plant (g)						
I	30.88±0.67	81.52±0.78	96.60±1.14	74.70±2.46	37.96±1.36	70.50±2.84
II	31.27±0.61	101.62±2.99	68.78±2.64	57.68±1.90	39.24±1.87	80.99±1.84
III	179.88±4.81	32.55±1.48	141.53±3.73	82.23±2.28	160.31±4.11	99.69±1.85
IV	103.02±4.30	45.57±2.09	118.75±1.90	99.90±1.31	100.32±1.16	56.12±1.37
V	106.56±1.55	88.55±1.39	117.11±1.69	99.00±1.49	105.50±2.41	95.30±1.59
Seed yield per plant (g)						
I	21.01±0.53	60.01±0.93	77.78±2.98	59.70±1.92	36.26±1.62	71.37±3.47
II	22.33±0.66	119.72±3.59	158.74±4.10	109.19±3.05	91.63±4.58	83.84±3.29
III	54.11±1.51	29.33±1.02	165.82±4.55	100.56±3.78	83.48±4.06	67.80±3.79
IV	46.51±2.15	58.08±2.10	81.25±1.98	79.13±2.36	63.00±2.63	67.50±2.31
V	107.87±3.56	90.76±2.54	128.08±3.55	97.96±3.51	108.79±4.31	112.43±4.86
Seed oil content (%)						
I	31.15±0.44	33.26±0.21	32.47±0.19	30.81±0.22	30.89±0.30	31.78±0.25
II	32.71±0.14	34.15±0.18	32.84±0.18	33.21±0.17	32.75±0.14	32.88±0.10
III	28.15±0.31	32.42±0.19	31.98±0.20	31.05±0.23	30.49±0.21	30.94±0.27
IV	33.04±0.18	33.43±0.16	33.69±0.12	32.30±0.15	32.98±0.18	31.85±0.14
V	32.15±0.26	32.66±0.29	33.38±0.17	32.38±0.17	31.45±0.24	30.84±0.28

Seed oil yield per plant (g)						
I	6.55±0.19	19.95±0.31	25.27±0.98	18.40±0.61	11.24±0.40	22.60±0.83
II	7.30±0.21	40.91±1.27	52.12±1.38	36.25±1.03	30.02±1.32	27.59±0.98
III	15.29±0.66	9.51±0.26	53.11±1.41	31.28±1.24	25.64±1.23	20.88±0.96
IV	15.35±0.71	19.43±0.73	27.38±0.81	25.53±0.76	20.83±0.90	21.58±0.81
V	34.72±1.24	29.61±0.82	42.75±1.43	31.82±1.20	34.19±1.33	34.72±1.62

Table 2: Estimates of simple scaling test and gene effects for different characters in *bidi* tobacco

Character	Cross	Scaling Test				χ^2 for Joint Scaling Test	Genetic Parameters						Type of Epistasis
		A	B	C	D		m	*d*	*h*	*i*	*j*	*l*	
Days to flowering	I	-6.85**	-18.75**	-15.00**	5.30**	64.49**	64.87**	-10.82**	-40.88**	-10.60**	11.90**	36.20**	Duplicate
	II	0.25	6.05**	11.70**	2.70*	30.77**	54.07**	-5.88**	-3.08	-5.40*	-5.80**	-0.90	
	III	4.40	1.80	-18.25**	-12.22**	24.87**	53.07**	34.03**	29.02*	24.45**	2.60	-30.65**	Duplicate
	IV	-10.10**	-8.30**	27.20**	22.80**	53.97**	108.87**	11.12**	-108.47**	-45.60**	-1.80	63.99**	Duplicate
	V	6.05**	0.25	9.40**	1.55	16.54**	63.92**	-4.02**	1.22	-3.10	5.80*	-3.20	
Leaves per plant	I	5.25**	0.50	0.20	-2.77**	121.47**	121.47**	8.89**	-3.30**	17.15**	5.55**	4.75**	Duplicate
	II	0.90	-1.00	1.90	1.00*	10.40*	10.40*	15.05**	-1.65**	-1.35	-2.00*	1.90*	Duplicate
	III	-18.80**	0.75	-16.90**	0.57	292.96**	292.96**	24.87**	12.83**	-25.82**	-1.15	-19.55	Duplicate
	IV	-4.20**	1.15*	-5.00**	-0.97	64.24**	64.24**	17.30**	1.85**	0.50	1.95	-5.35**	Duplicate
	V	3.05**	0.25	0.45	-1.42**	24.68**	24.68**	11.85**	-0.40*	11.40**	2.85**	2.80**	Duplicate
Plant height	I	8.25**	-19.00**	-0.15	5.30**	109.28**	109.28**	107.45**	-18.50**	-18.60**	-10.60**	27.25**	Duplicate
	II	52.20**	13.80**	62.05**	-1.97	460.72**	460.72**	98.27**	-27.98**	88.37**	3.95	38.40**	Duplicate
	III	55.40**	96.25**	141.90**	-4.87	2172.71**	2172.71**	112.69**	48.40**	125.15**	9.75	-40.85**	Duplicate
	IV	20.25**	-3.70	9.10	-3.72	53.72**	53.72**	100.95**	11.52**	11.85	7.45	23.95**	
	V	5.70**	8.90**	-18.30**	-16.45**	112.26**	112.26**	90.42**	8.47**	64.38**	32.90**	-3.20	
Branches per plant	I	0.00	0.80	-0.55	-0.65	6.06	5.55**	-0.80**	0.20	TPM			
	II	-1.90**	0.30	1.35	1.47**	29.22**	10.30**	-2.60**	-6.00**	-2.95**	-2.20**	4.55**	Duplicate
	III	2.95**	-0.40	2.85**	0.15	57.83**	7.32**	2.53**	1.97	-0.30	3.35**	-2.25*	
	IV	-0.50	1.10**	4.10**	1.52**	41.17**	10.47**	0.27	-3.22	-3.05**	-1.15*	1.99	
	V	-1.75**	-0.50	-4.30**	-1.02*	24.12**	7.47**	0.68**	3.37	2.05*	-1.25	0.20	
Capsules per plant	I	50.30	-216.00**	131.10	148.40**	65.60**	686.55**	-150.80**	-666.65**	-296.80**	266.30**	462.49**	Duplicate
	II	-96.25**	-437.05**	-386.20**	73.55**	191.57**	485.70**	-144.20**	-502.10**	-147.10**	340.80**	680.40**	Duplicate
	III	-140.65**	-351.95**	19.70	256.15**	53.40**	736.45**	23.70**	-1057.24**	-512.30**	211.30**	1004.92**	Duplicate
	IV	-9.85	-47.40	-350.40**	-146.57**	41.30**	-2.28	-91.42**	844.37**	293.15**	37.54	-235.90	
	V	-68.20	-79.80*	-385.90**	-118.95**	37.99**	268.38**	-37.73**	335.70*	237.89**	11.60	-0.90	
Days to capsule maturity	I	24.75**	-0.85	18.45*	-2.72	40.19**	70.55**	-24.75**	38.84	5.44	25.60**	-29.34*	
	II	5.85*	21.30**	31.60**	2.22	29.18**	96.20**	-38.70**	27.24	-4.45	-15.45**	-22.70	
	III	-5.20	2.35	-33.30**	-15.22**	17.67**	68.27**	45.17**	48.32	30.45*	-7.55	-27.60	
	IV	-19.30**	-12.05**	-42.35**	-5.50	22.14**	96.49**	34.05**	-22.74	11.00	-7.25	20.35	
	V	-0.85	-14.85**	29.25**	22.47**	61.35**	167.12**	10.72**	-96.86**	-44.94**	14.00**	60.65**	Duplicate
Capsule weight	I	47.96**	30.17*	57.26*	-10.43	9.82*	243.48**	-7.44*	188.11**	20.85	17.79	-98.98*	Duplicate
	II	70.83**	-17.46	231.31**	88.97**	130.92**	474.28**	-43.02**	-271.44**	-177.94**	88.30**	12.46**	Duplicate
	III	-45.12*	83.44**	-24.76	-31.54	24.84**	214.52**	23.62**	218.24*	63.07	-128.56**	-101.39**	Duplicate
	IV	-45.88**	73.60**	-87.22**	-57.47**	61.28**	188.77**	41.70**	293.19**	114.93**	-119.48**	-142.65**	Duplicate
	V	-6.29	-104.05**	-99.51**	5.41	24.06**	363.52**	-37.32**	-141.67**	-10.83	97.76**	121.16**	Duplicate
Seed weight per capsule	I	110.01**	116.40**	211.19**	-7.61	183.50**	128.07**	4.25	321.35**	15.22	-6.40**	-241.63**	Duplicate
	II	89.72**	-12.75	206.82**	64.93**	189.52**	327.20**	-50.41**	-141.07*	-129.86**	102.47**	52.90	
	III	-32.94*	100.92**	21.93	-23.02	53.10**	136.60**	37.24**	219.30**	46.03	-133.86**	-114.00**	Duplicate
	IV	-13.50	91.73**	-5.68	-41.95**	81.98**	108.79**	39.44**	301.04**	83.91**	-105.24**	-162.15**	Duplicate
	V	-4.60	-39.96	-37.65	3.95	6.96	231.65**	-2.10	13.03	TPM			
Test weight	I	-11.86**	-11.40**	-36.44**	-6.48**	108.06**	50.72**	-4.68**	6.27	12.98**	-0.26	10.49	
	II	4.75	-3.70	-4.80	-2.93	7.72	60.11**	0.11	7.42**	TPM			
	III	-6.05	1.49	-11.67	-3.03	7.73	57.94**	-1.58*	13.27**	TPM			
	IV	0.88	-3.04	-30.87**	-14.36**	35.33**	27.41**	-9.16**	52.61**	28.72**	3.93	-26.57**	Duplicate
	V	-4.65	3.60	-14.76**	-6.86**	20.37**	49.80**	-4.89**	28.51	13.73**	-8.23	-12.72	
Leaf yield per plant	I	-51.57**	-37.11**	-6.82	40.93**	309.69**	138.06**	-25.32**	-212.02**	-81.86**	-14.45*	170.55**	Duplicate
	II	-21.56**	-8.43	-39.74**	-4.87	18.87**	56.70**	-35.17**	-8.17	9.75	-13.14	20.25	
	III	-0.78	25.30**	-166.55**	-95.53**	240.76**	-84.86**	73.66**	441.98**	191.07**	-26.09*	-215.60**	Duplicate
	IV	-21.13**	-52.08**	13.51	43.36**	250.89**	161.03**	28.73**	-202.22**	-86.73**	30.96**	159.95**	Duplicate
	V	-12.66	-15.04**	-33.34**	-2.81	28.11**	91.92**	9.00**	3.11	5.64	2.39	2.21	
Seed yield per plant	I	-26.27**	4.95	2.20	11.75*	46.64**	64.02**	-19.50**	-31.06	-23.51*	-31.23**	44.82*	
	II	2.18	-110.77**	-22.76	42.91**	187.81**	156.86**	-48.69**	-192.56**	-85.84**	112.96**	194.43**	Duplicate
	III	-51.71**	-59.55**	-12.33	49.46**	41.33**	140.65**	12.39**	-185.04**	-98.94**	7.83	210.20**	Duplicate
	IV	-1.76	-4.33	49.42**	27.76**	17.55**	107.82**	-5.78**	-88.19**	-55.53**	2.56	61.62**	Duplicate
	V	-18.37	6.02	-62.96**	-25.30**	16.56**	48.69*	8.56**	117.65**	50.62**	-24.39	-38.26	
Seed oil content	I	-1.83*	-2.16**	-6.13**	-1.06	41.15**	30.07**	-10.56**	0.53	2.13	0.33	1.87	
	II	-0.05	-1.23**	0.28	0.78	18.40**	35.00**	-0.72**	-5.02**	-1.57*	1.18**	2.86**	Duplicate

	III	0.86	-2.52**	-0.34	0.66	21.24**	31.60**	-2.14**	-2.61	-1.33	3.38**	2.99	
	IV	-0.76	-3.42**	-4.65**	-0.23	59.06**	32.77**	-0.19	-0.28	0.46	2.65**	3.73*	
	V	-2.63**	-4.35**	-2.03**	2.48**	56.28**	37.36**	-0.25	-15.94**	-4.96**	0.17	0.12**	Duplicate
Seed oil yield per plant	I	-9.43**	-0.02	-3.43	3.01	49.72**	19.27**	-6.70**	-9.50	-6.03	-9.41**	15.48**	
	II	0.62	-37.85**	-7.44	14.89**	197.10**	53.88**	-16.80**	-68.78**	-29.78**	38.47**	67.02**	Duplicate
	III	-17.13**	-20.86**	-5.90	16.04**	47.08**	44.48**	2.89**	-61.44**	-32.08**	3.73	70.07**	Duplicate
	IV	-1.07	-3.64	12.57**	8.65**	16.24**	34.69**	-2.04**	-29.33**	-17.30**	2.57	22.02**	Duplicate
	V	-9.10**	-2.91	-22.54**	-5.26	17.75**	21.64**	25.58**	19.62	10.53	-6.20	1.49	

*,** Significant at 5 and 1 per cent levels of probability, respectively. TPM – Three Parameters Model.

4.3 Plant height

The perusal of results of different crosses revealed significant estimated of gene effects *d*, *h*, *i*, *j* and *l* which indicated the involvement of additive, dominance as well as epistatic interactions, and the components (h) and (l) had opposite signs revealed the existence of duplicate epistasis in the inheritance of plant height. The greater magnitude of dominance gene action was observed for this trait. Ramachandra *et al.* (2005) [14] and Katba *et al.* (2019) [4] reported consequences of both additive and non-additive gene actions for expression of this trait.

4.4 Branches per plant

Additive gene effect played a vital role in all crosses except cross III which exhibited involvement of both additive and non-additive gene effects in inheritance of this trait. As branches per plant had additive gene control in majority of crosses, pedigree method of breeding could profitably be used for further improvement in this trait. Preponderance of additive gene effect for this trait was also observed by Patel (2009) [12] and Pawar (2010) [13].

4.5 Capsules per plant

The presence of additive and non-additive gene actions in all crosses suggested that reciprocal recurrent selection or biparental mating in F_2 or subsequent generations may be employed for further improvement of the character. The opposite signs of dominance (h) and dominance × dominance (l) exhibited duplicate type of epistasis in crosses I, II and III. Similar results were obtained by Patel (2005) [11] and Hadiya *et al.* (2017) [3] in the expression of this trait.

4.6 Days to capsule maturity

The crosses I and V exhibited additive as well as non-additive gene effects responsible for the inheritance of this trait, which is in line with the results of Patel (2005) [11] and Hadiya *et al.*, (2017) [3]. The preponderance of additive gene effects was observed in crosses II, III and IV and pedigree method would be more effective in improvement of this trait. The present findings are in close agreement with the results obtained by Patel (2009) [11] and Pawar (2010) [13]. A duplicate type of non-allelic gene interaction was involved in cross V i.e. A 119 × L 108-15-3.

4.7 Capsule weight

Considering the capsule weight, two principle gene effects i.e. additive (*d*) and dominance (*h*) and all interaction effects namely additive × additive (*i*), additive × dominance (*j*) and dominance × dominance (*l*) were found equally important for the inheritance of this trait in all crosses. The opposite signs of the components (*h*) and (*l*) showed the duplicate type of epistasis in all the crosses. Similar result was reported by Hadiya *et al.* (2017) [3] for inheritance of capsule weight in *bidi* tobacco.

4.8 Seed weight per capsule

The involvement of fixable and non-fixable gene effects for inheritance of the seed weight per capsule in crosses I, II, III and IV suggest that cyclic method of breeding involving selection of superior gene types and their inter se crossing would be profitably utilized to take advantage of both additive and non-additive type of gene actions for improvement of this trait. However, in cross V involvement of dominance gene effect suggested heterosis breeding could be profitably utilized for the improvement of this trait. Role of additive and non-additive gene actions for seed weight per capsule was earlier reported by Hadiya *et al.* (2017) [3].

4.9 Test weight

The individual scaling test were non-significant in crosses II and III which suggested adequacy additive-dominance model, and dominance gene effect was predominant in the inheritance of this trait in these crosses. Additive (*d*) gene effect along with additive × additive (*i*) interactions were found significant in crosses I and V, whereas all types of gene effects except additive × dominance (*j*) interaction were significant in cross IV and the *h* and *l* gene effects recorded opposite signs in this cross which indicated duplicate type of epistasis. Patel (2009) [12] and Pawar (2010) [13], and Hadiya *et al.* (2017) [3] opined the participation of dominance and additive gene effects for this trait, respectively.

4.10 Leaf yield per plant

Additive gene effect (*d*) was responsible for the expression of this trait in crosses II and V, while both additive and non-additive gene effects were responsible for the inheritance of this trait in crosses I, III and IV. Crosses I, III and IV exhibited duplicate type of epistasis for leaf yield per plant. Patel (2005) [11], Pawar (2010) [13] and Hadiya *et al.* (2017) [3] reported role of both additive and non-additive gene effects for the leaf yield per plant.

4.11 Seed yield per plant

Involvement of both additive and non-additive gene effects were found in expression of this trait in all crosses which suggested that bi-parental mating or reciprocal recurrent selection would be effective for improvement of seed yield. A duplicate type of non-allelic interaction were involved in crosses II, III and IV. The presence of additive, dominance and epistatic interactions in the inheritance for this trait were earlier reported by Patel (2005) [11] and Hadiya *et al.* (2017) [3].

4.12 Seed oil content

Both additive and dominance gene effects, and higher order interaction were found significant in cross II. Only additive (*d*) gene effect was significant in cross I and higher magnitude of additive gene action was observed in cross III. The significant values of additive × dominance (j) and dominance × dominance (l), and dominance (*h*), additive × additive (*i*) and dominance × dominance (*l*) indicated preponderance of dominance gene effect in cross IV and V, respectively. Preponderance of dominance

gene effect for this trait was also observed by Patel (2009) [12], Pawar (2010) [13] and Hadiya *et al.* (2017) [3] while role of additive and dominance gene effects for this trait was reported by Patel (2005) [11].

4.13 Seed oil yield per plant

For inheritance of this trait, additive and non-additive gene effects played vital role in crosses I, II, III and IV, where homozygous elite recombinants could be developed following inter se crossing of desirable segregants; while additive gene effect was found in cross V, where pedigree method of breeding, would be more appropriate for further improvement. Role of additive and non-additive gene actions were earlier reported by Patel (2005) [11] and Hadiya *et al.* (2017) [3]; whereas Patel (2009) [12] and Pawar (2010) [13] found additive gene action responsible for the inheritance of this trait.

Conclusion

A few of the seed oil yield attributing characters like seed oil content, test weight and seed oil yield per plant in crosses like Dediapada Selection × A 145 (cross I) and A 119 × L 108-15-3 (cross V) which are governed by additive (*d*) and additive × additive (*i*) gene interaction effects are fixable. In these crosses Pedigree method of breeding followed by selection in later segregating generations will be most useful strategy for the improvement of important seed oil yield attributing characters mentioned above. In other character-cross combinations, recurrent selection by way of intermating the desirable segregants followed by selection, diallel selective mating or the use of multiple crosses and biparental mating might prove to be effective alternative approaches where non-additive gene actions including epistatic interaction effects found significant.

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