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RESEARCH ARTICLE

Generation of biparental progenies and dissection of gene action for yield and related traits in lentil (*Lens culinaris* L. Medikus)

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Abstract

Lentil (*Lens culinaris* L. Medikus), commonly known as 'masoor', is one of the major cool-season food legumes. The present investigation was aimed at creating new genetic variability through biparental mating-derived progenies and studying the nature and magnitude of gene effects for yield and component traits. Biparental progenies were developed from three lentil crosses viz., PL 6 x PL 8; PL 6 x L 4147 and L 4147 x PL 7 and were evaluated alongwith $F_{2:3}$ progenies in the field. The resulting progenies released useful genetic variability including transgressive segregants. The magnitude of dominance genetic variance was higher than the additive genetic variance for traits viz. days to 50% flowering, days to maturity, number of primary branches per plant, number of secondary branches per plant, plant height (cm), number of pods per plant, seed diameter (mm), seed yield per plot (g), biological yield per plot (g) and harvest index. Hybridization followed by selection at later generations is suggested for exploiting dominance gene action in these traits. Hundred seed weight was the only parameter in which additive variance was greater than dominance variance and also showed the highest heritability in all three crosses. Therefore, preference should be given to pure line selection, mass selection and/or progeny selection for improvement of 100-seed weight.

Introduction

Globally, lentil (*Lens culinaris* L. Medikus) ranks fourth among the major pulses after dry bean, pea and chickpea in terms of production with world lentil production of 5.7 mt, which was approximately 8% of the total production of dry pulses. In India, lentil is the second most important *rabi* crop after chickpeas grown under a 1.63 m ha area with a production of 1.56 mt (FAO STAT 2023). Lentil demand is skyrocketing around the world as more and more people are transitioning to a vegetarian diet. However, lentil yields have remained stable over the last 2-3 decades, hovering about 10 to 12 q/ha. As a result, high-yielding lentil cultivars are urgently needed to meet the growing demand (Kumar et al. 2016). Lentil has a relatively short organized breeding history compared to most of the other major crops because lentil domestication and cultivation have historically relied on landraces and traditional varieties rather than systematic breeding efforts. (Materne and Mc Neil 2007).

The pedigree method of selection is commonly practiced in crops because the genes for desirable characters are rapidly fixed in a homozygous state however, the desired recombination among linked genes is limited (Humphrey et al. 1989). This procedure is inadequate to explore the range of useful existing genetic variability for complex characters like yield. Inter-mating of randomly selected plants

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from early segregating generations breaks undesirable linkage that would help create new populations with high frequencies of rare recombinants. Of the various methods of improving the frequency of desirable recombinants, biparental mating as suggested by Comstock and Robinson (1948, 1952), which is based on the assumption that it may convert repulsion phase linkages into coupling phase due to forced recombination, releasing a greater amount of concealed genetic variation, particularly of the additive type that can help in effective selection (Chandrakant et al. 2015). Variability thus generated could be utilized for the improvement of autogamous crops (Singh and Sharma 1983). Further, to understand the nature and magnitude of gene effects involved in the inheritance of agronomically important characters, three approaches namely, diallel analysis, generation mean analysis and line x tester analysis have been used in the past to illustrate gene action involved in the expression of different quantitative traits (Khodambashi et al. 2012; Singh et al. 2018; Verma et al. 2022). Although these genetic analysis approaches are reliable and informative, they restrict change in recombination rates and retain tight linkage that can lead to biases in genetic interpretation (Brim and Cockerham 1960). The estimation of genetic components (Additive and dominance variance) and narrow sense heritability ($h^{2)}$ is more realistic under the North Carolina-III design as compared to other approaches (Kearsey 1980; Vinayan and Govindarasu 2010). The present study was, therefore, conducted to generate genetic variability adopting biparental mating and to understand the nature and magnitude of gene effects for agronomically important traits. To our knowledge, the present article represents the first report on the estimation of genetic variances by using the North Carolina-III design in lentil crops.

Materials and methods

Experimental material and field trials

The four lentil genotypes consisting of two bold seeded (PL 6 and PL 7) and two small seeded (PL 8 and L 4147) were crossed to produce three different single cross hybrids: (1). PL 6 x PL 8, (2). PL 6 x L 4147 and (3). L 4147 x PL 7 at Norman E. Borlaug Crop Research Centre of the G. B. Pant University of Agriculture and Technology, Pantnagar (Uttarakhand), India (29.5^0 N and 79.3^0 E). The pedigree information of the parents along with their other morphological features is provided in Supplementary Table S1. The generated F_2 populations from these crosses were raised in non-replicated rows. Biparental progenies were generated from F_2 generation of inter-varietal cross using North Carolina Design III (Comstock and Robinson (1948, 1952). The biparental progenies were developed by designating 4 random F_2 plants as males and backcrossing each of them to both parents. Eight progenies generated in this way make up one set and likewise, three sets were generated from each cross. Thus, a total of 72 biparental progenies (24 from each cross) were generated in this investigation. The selected F_2 plants were also selfed to produce F_2-derived F_3 families ($F_{2:3}$). Biparental progenies and $F_{2:3}$ families were evaluated during the next *rabi* season in randomized block design (RBD) with two replications. The schematic representation of the crossing plan is given in Supplementary Fig. 1. All the recommended packages of practices were followed to raise a normal and healthy crop.

Observations recorded

The observations were recorded on five randomly selected competitive plants from each replication on characters namely, plant height (cm), number of primary branches per plant, number of secondary branches per plant, number of pods per plant, number of pods per cluster, number of seeds per pod, 100-seed weight (g), seed yield per plant (g), biological yield per plant (g) and harvest index. However, the data on the number of days to 50% flowering and number of days to maturity were taken on a whole plot basis. Days to maturity were recorded from sowing to when 90% of pods turned golden brown. The seed diameter (mm) was calculated as the average length of 10 seeds placed in a row measured on a centimeter scale. The mean value of each character from each replication was used for statistical analysis.

Statistical analysis

After ascertaining the significant difference among the BIPs using RBD, the mean data were subjected to analysis of variance appropriate to North Carolina design III as given by Comstock and Robinson (1952). Components of genetic variance and average degree of dominance were estimated as per the method provided by Comstock and Robinson (1948, 1952). Narrow sense heritability was calculated using a formula suggested by Allard (1960). Genetic advance as a percent of the mean for each character was worked out as suggested by Johnson et al. (1955). The data were analyzed using the INDOSTAT software (IndoStat Inc. Hyderabad, India) to estimate different components of genetic variances.

Results and discussion

Data from parents, F_1, F_2, $F_{2:3}$ and biparental progenies generated through North Carolina Design-III was studied using the parameters viz., range, mean, standard deviation and coefficient of variation as presented in Tables 1, 2 and 3. In general, the mean values of biparental populations (BIPs) were higher than the corresponding mean values of parents, F_2 and $F_{2:3}$ generations for most of the characters except day to 50% flowering and day to maturity in cross 2 and plant height in cross 3. In cross 2, the days to flowering and days to maturity were considerably reduced in BIP than in parent 1, F_1, F_2, and $F_{2:3}$ generation. Thus, biparental mating introduced additional variability for maturity

Table 1. Mean data of parents, F1, F2, F3 and biparental progenies (PL6 X PL 8)

Parameters	DTF	DM	PH	NPB	NSB	NPP	NPC	NSP	SD	HSW	BYP	SYP	HI
P1	78.50	123.30	27.12	2.40	4.04	52.60	1.90	1.80	4.20	2.30	3.51	1.11	0.35
P2	84.05	130.10	31.00	3.16	7.21	61.00	2.10	1.65	3.35	2.13	5.70	2.12	0.38
F1	85.10	132.5	31.10	3.85	8.50	78.00	2.12	1.82	4.44	2.28	5.60	2.33	0.41
F2	82.25	125.0	29.47	2.74	6.24	60.1	1.90	1.70	3.40	2.19	5.00	1.80	0.36
Range	77.40–84.6	120.3–131.6	25.00–32.01	1.41–4.72	4.00–8.50	35.81–90.32	1.33–2.94	1.45–1.98	2.89–4.12	1.87–3.24	3.47–6.95	1.31-2.95	0.22-0.58
SD	2.67	4.84	3.42	0.89	3.57	15.12	0.35	0.27	0.25	0.43	0.35	1.26	0.06
F3	80.14	123.50	28.14	2.69	6.10	55.65	1.91	1.66	3.69	2.15	4.62	1.76	0.38
Range	79.00–84.00	122.3–132.0	26.81–30.54	2.00–4.10	5.02–7.61	30.52–74.25	1.45–2.5	1.42–1.88	2.97–4.02	1.82–2.97	4.20–5.65	1.45-2.64	0.27-0.51
C.D	2.553	3.037	4.165	1.065	4.927	18.315	0.375	N/A	0.405	0.469	1.04	0.436	0.1
SE (m)	0.811	0.964	1.322	0.338	1.564	5.815	0.119	0.144	0.129	0.149	0.33	0.138	0.032
SE (d)	1.146	1.364	1.87	0.478	2.212	8.223	0.169	0.204	0.182	0.21	0.467	0.196	0.045
C.V.	1.426	1.075	6.224	11.023	19.664	9.692	8.653	11.342	4.464	9.761	8.862	12.244	14.879
BIP	81.00	126.54	29.24	3.43	7.65	72.86	2.00	1.78	4.15	2.20	5.13	2.11	0.40
Range	75–85	119–136	20–36	3–6	4–20	30–125	1.3–2.5	1.16–2.0	3.5–7.8	1.4–3.2	3.40–7.60	1.04-2.50	0.18-0.45
C.D	2.734	3.00	5.97	1.23	3.89	14.41	0.40	N/A	0.46	0.58	1.47	0.38	0.11
SE (m)	0.929	1.02	2.03	0.42	1.32	4.90	0.14	0.158	0.16	0.20	0.50	0.13	0.04
SE (d)	1.313	1.44	2.87	0.59	1.87	6.93	0.19	0.223	0.22	0.28	0.71	0.18	0.05
C.V.	1.62	1.12	9.75	13.32	17.57	10.39	10.17	13.27	5.32	12.27	13.75	11.32	16.01

Table 2. Mean data of parents, F1, F2, F3 and biparental progenies (PL 6 X L4147)

Parameters	*DTF*	*DM*	*PH*	*NPB*	*NSB*	*NPP*	*NPC*	*NSP*	*SD*	*HSW*	*BYP*	*SYP*	*HI*
P1	78.50	123.30	27.91	2.40	4.04	52.60	1.90	1.80	4.20	2.30	3.15	1.51	0.36
P2	82.50	131.33	34.00	2.66	3.70	65.00	2.30	1.69	3.87	2.18	4.40	1.71	0.38
F1	85.21	133.40	36.80	4.67	10.81	80.81	2.14	1.92	4.55	2.91	6.61	2.39	0.39
F2	81.50	129.60	33.24	3.69	7.61	53.69	2.12	1.74	3.90	2.29	5.31	1.93	0.36
Range	76.30–84.16	120.1–133.41	20.34–42.10	1.52–3.60	2.10–7.90	26.25–70.64	1.30–2.64	1.34–2.31	2.90–4.58	1.54–3.41	3.69–7.81	1.25–2.64	0.19–0.54
SD	2.52	3.76	3.88	1.08	1.97	25.25	0.22	1.76	0.45	0.62	0.79	0.30	0.04
F3	79.34	126.25	31.91	3.31	7.36	59.23	1.95	1.65	4.01	2.22	5.26	1.84	0.34
Range	78.00–84.21	122–133.20	22.60–40.21	1.68–3.51	2.49–6.81	30.50–71.69	1.39–2.48	1.54–2.17	3.40–4.37	1.61–2.59	3.85–7.42	1.42–2.63	0.21–0.51
C.D	3.52	3.88	5.61	1.22	3.14	21.87	N/A	N/A	0.56	0.67	0.96	0.33	0.06
SE (m)	1.12	1.23	2.44	0.54	1.13	6.94	0.19	0.23	0.18	0.21	0.30	0.10	0.03
SE (d)	1.58	1.74	3.44	0.77	1.59	9.82	0.35	0.33	0.25	0.30	0.43	0.15	0.02
C.V.	1.96	1.34	12.85	18.83	15.78	13.06	13.30	19.61	6.24	14.27	9.15	9.75	7.81
BIP	77.94	122.60	35.21	4.31	9.40	78.75	1.94	1.80	4.15	2.86	6.57	2.49	0.37
Range	74–86	121–139	18–37	2.9–7.2	6.1–14.2	20–125	1.25–2.60	1.2–2.7	2.90–4.70	1.20–3.42	2.93–7.41	1.08–2.40	0.25–0.45
C.D	3.36	4.64	6.63	1.74	2.91	36.57	N/A	N/A	0.63	0.70	1.14	0.35	0.06
SE (m)	1.14	1.58	2.25	0.59	0.99	12.43	0.18	0.20	0.21	0.24	0.39	0.12	0.02
SE (d)	1.62	2.23	3.19	0.83	1.40	17.57	0.25	0.29	0.30	0.33	0.55	0.17	0.03
C.V.	2.00	1.72	11.72	19.33	13.45	22.31	12.90	16.44	7.46	16.22	11.98	11.11	9.14

duration allowing selection of early genotypes. It was also found that in BIPs of all three crosses, seed yield per plant was significantly improved when compared to parents, F_2 and $F_{2:3}$ generations. Moreover, yield per plant in BIP of cross 1 was even greater than the corresponding F_1 generation. The superior performance of biparental progenies over $F_{2:3}$ could be the result of considerable heterozygosity in biparental progenies and of inbreeding depression in $F_{2:3}$ progenies (Gardner et al. 1953). This is critical for breeders, as the mean of populations decreases progressively from the F_2 generation as homozygosity increases from F_3 generation onward. Enhancement in the trait mean value might be due to pooling of favorable alleles or reshuffling of the alleles through recombination which was possible because of biparental mating. Reshuffling of alleles due to biparental mating certainly helps in the better exploitation of the non-additive gene effect that results in the increase in mean performance. The upper limit of range values was higher in biparental populations (BIPs) than the corresponding value in $F_{2:3}$ for most of the component traits including yield itself and also individual plants having higher grain yield compared to the parental varieties were identified in all three BIPs. This confirmed the presence of transgressive segregants in BIPs. Also, the lower limit of the range in all three BIPs was foreshortened than the corresponding value in $F_{2:3}$ for all the traits. The wider range values compared to the corresponding $F_{2:3}$ populations indicated that biparental mating has helped in releasing more variability than selfing. Furthermore, the value of the phenotypic coefficient of variation (CV) was higher in BIPs as compared to the $F_{2:3}$ populations for all the characters. The increase in variability in biparental populations might be due to the breakage of undesirable linkage (Gill et al. 1973; Vinayan and Govindarasu 2010). Similar results using biparental mating were also obtained by Kampli et al. (2002) in chickpeas. The variability and transgressive segregants obtained in the present investigation can help to break the yield plateau in lentils.

Data generated was subjected to analysis of variance appropriate for NC-III biparental mating design. The results of ANOVA revealed statistically significant differences in the mean sum of squares due to females as well as males in sets in all three crosses for all studied traits except the number of pods per cluster and the number of seeds per pod (Supplementary Table S2). The significance of these traits suggested that the parents used for the production of biparental progenies were significantly different from each other concerning these traits. The mean sum of squares due to interaction in sets was also found significant for all traits except the number of pods per cluster and the number of seeds per pod. These results indicated the presence of sufficient genetic variability in the experimental material allowing further investigation of gene action involved in the expression of respective traits. However, for the trait number of pods per cluster and number of seeds per pod variability recorded was not significant. The present findings are contrary to the earlier findings that recorded significant variability in their study for traits number of pods per cluster and number of seeds per pod in lentils. Kumar et al. (2009) investigated advanced (F_6) generation derived from microsperma x macrosperma crosses and observed ample variability for all the characters except seeds per pod.

Estimates of genetic parameters for various taris in three crosses are presented in Table 4. In all crosses, additive and dominant genetic variation was found to be significant for all of the traits except traits seeds per pod and pods per cluster. These results indicate the importance of both additive and dominance variance in controlling the expression of these traits in lentils. Similar results were obtained by Kumar et al. (2011) in lentils using triple test cross analysis. They found that mean squares due to sums and differences were significant for all traits except seeds per pod and methionine content, which provide a direct test of significance for additive and dominant components of variation. No negative estimates of variance components were observed in the present investigation. This is because of the small magnitude of standard error associated with estimates of variance. Negative estimates of variance were earlier reported by many researchers (Maurya et al. 2011; Kumar et al. 2007; Abbas et al. 2016) using mating designs other than NCD III. In general, the variance estimates for crosses with more differing parents for concerning traits were higher. In cross 1, parents were relatively more differing with respect to traits viz. primary branches per plant, secondary branches per plant, biological yield per plant and seed yield per plant resulting in higher variance estimates compared to crosses, 2 and 3. Haddad et al. (1982) examined three lentil crosses using a hierarchical design from the F_2 to the F_5 generations and discovered that the variance estimates were higher in cross Tekoa x P1212611, where the parents differed the most in terms of measured characters such as days to blooming, days to maturity, plant height, height of lowest pod, plant type and seed weight.

The estimates of dominance variance were significantly greater than additive variance in all three crosses, except for 100-seed weight where additive variance was found to be more than the dominance variance. These results were further confirmed by the degree of dominance which was greater than unity for most of the studied traits except 100-seed weight. The more than unity degree of dominance ratio indicated the presence of over-dominance for most of the studied traits however, for 100-seed weight, it indicated partial dominance or incomplete dominance.

The highest average degree of dominance was noticed for trait seed yield per plant followed by harvesting index in the cross, PL 6 X L4147. The presence of dominant genetic variance for these traits in lentils was also reported earlier

Table 3. Mean data of parents, F1, F2, F3 and biparental progenies (L4147 X PL 7)

Parameters	*DTF*	*DM*	*PH*	*NPB*	*NSB*	*NPP*	*NPC*	*NSP*	*SD*	*HSW*	*BYP*	*SYP*	*HI*
P1	82.01	131.10	34.00	2.66	3.70	40.00	2.30	1.89	3.87	2.28	4.40	1.71	0.38
P2	79.20	125.02	28.31	2.73	5.10	55.00	1.60	1.59	4.02	2.47	4.70	1.92	0.40
F1	83.60	135.6	40.35	4.10	10.64	85.09	2.84	2.18	4.65	2.95	6.89	3.01	0.43
F2	82.64	133.10	35.61	3.91	8.61	60.35	2.32	1.99	4.11	2.51	5.51	2.12	0.38
Range	72.12–85.64	120.25–136.21	25.69–42.31	1.52–5.61	2.25–11.64	24.81–85.61	1.20–2.99	1.21–2.2	3.10–4.69	1.65–3.41	3.14–7.64	1.10–4.37	0.19–0.61
SD	2.264	2.814	5.768	1.121	1.825	18.239	0.310	0.283	0.359	0.550	1.105	0.650	0.078
F3	81.89	131.02	35.14	3.83	8.14	62.51	2.14	1.85	4.10	2.48	5.32	1.87	0.39
Range	71.36–84.64	124.30–133.14	28.14–36.45	1.68–5.11	3.51–10.84	28.21–82.41	1.54–2.85	1.37–2.10	3.21–4.41	1.66–3.37	3.06–6.87	1.28–3.47	0.18–0.51
C.D	2.14	2.672	6.453	1.249	2.601	18.916	N/A	N/A	0.415	0.572	1.54	0.31	0.072
SE (m)	1.27	0.848	2.049	0.396	0.826	6.006	0.163	0.178	0.203	0.182	0.441	0.126	0.023
SE (d)	1.795	1.2	2.897	0.561	1.168	8.493	0.231	0.252	0.287	0.257	0.623	0.179	0.032
C.V.	2.26	0.937	10.077	11.702	11.034	10.589	12.704	15.036	6.746	10.983	11.922	7.769	7.49
BIP	82.65	134.52	33.00	3.92	10.33	78.02	2.40	1.68	4.15	2.60	6.19	2.00	0.42
Range	73–84	120–135	20–39	2.1–7.2	7.2–14	40–111	1.30–2.50	1.16–2.0	3.50–4.90	1.20–3.20	3.10–7.32	1.02–3.10	0.28–0.58
C.D	3.431	4.852	5.934	1.502	2.901	21.052	0.463	N/A	0.541	0.559	1.614	0.399	0.128
SE (m)	1.165	1.648	2.016	0.51	0.985	7.152	0.157	0.163	0.184	0.19	0.548	0.136	0.044
SE (d)	1.648	2.331	2.851	0.722	1.394	10.114	0.223	0.23	0.26	0.269	0.775	0.192	0.062
C.V.	2.069	1.828	9.83	15.964	13.486	12.963	11.741	13.678	6.27	11.699	14.956	8.338	14.268

Table 4. The estimates of genetic variances and variability parameters

Characters	Crosses	σ^2ml	σ^2m	σ^2D	σ^2H	σ^2E	DD	h^2_{NS}	GA as (%) of mean
DFF	C1	5.18**	1.29*	5.18*	10.37**	1.00*	2.00	31.29	3.23
	C2	2.84*	0.92**	3.66**	5.68*	1.22**	1.55	34.67	2.85
	C3	5.17**	1.31*	5.25*	10.36**	1.44*	1.97	30.81	3.29
DM	C1	1066**	2.47*	9.89*	21.32**	1.24*	2.16	30.47	2.79
	C2	6.05*	1.53*	6.12*	12.10*	2.58*	1.98	29.41	2.14
	C3	9.82**	2.35*	9.38*	1963**	4.28*	2.09	28.18	2.63
PH	C1	16.00**	3.84*	15.35*	31.99**	3.58*	2.08	30.14	15.70
	C2	16.04**	4.10*	16.41*	32.04**	2.39*	1.95	32.25	17.42
	C3	14.92**	3.58*	14.31*	29.84**	2.39*	2.09	30.74	14.90
NPB	C1	1.28**	0.31*	1.22*	2.55**	0.15**	2.10	31.13	28.87
	C2	1.86**	0.51**	2.04**	3.72**	0.20***	1.82	34.26	39.91
	C3	0.81*	0.25*	0.99*	0.61*	3.02**	1.62	32.93	25.59
NSB	C1	10.15**	2.17*	8.68*	20.31**	1.95*	2.34	28.05	30.19
	C2	6.44**	1.28*	5.10*	12.88**	0.49	2.45	27.62	23.52
	C3	2.71*	0.85**	3.39**	5.42*	0.97**	1.60	34.66	21.60
NPP	C1	454.07**	114.87*	459.46**	908.14**	43.10**	1.98	32.57	30.53
	C2	249.90**	61.04*	244.04*	499.79**	71.54**	2.05	29.94	19.72
	C3	259.84**	51.11*	204.45*	519.68**	24.01*	2.54	27.33	19.74
NPC	C1	0.01	0.01	0.04	0.03	0.12	0.66	22.29	25.92
	C2	0.06	0.02	0.09	0.11	0.09	1.31	29.84	25.86
	C3	0.04	0.02*	0.10*	0.08*	0.06*	0.85	40.44	23.27
NSP	C1	0.03	0.01	0.03	0.05	0.05	1.78	22.84	36.89
	C2	0.01	0.01	0.02	0.03	0.06	1.19	22.49	25.81
	C3	0.02	0.002	0.01	0.03	0.04	4.39	7.96	23.40
SD	C1	0.06*	0.02**	0.09**	0.11*	0.02*	1.26	40.3	9.46
	C2	0.15*	0.06**	0.25**	0.30*	0.06**	1.21	40.91	16.27
	C3	0.07*	0.03**	0.12**	0.14*	0.04**	1.16	39.96	10.93
HSW	C1	0.14**	0.09**	0.36**	0.28**	0.03*	0.76	54.61	40.36
	C2	0.18*	0.13**	0.52**	0.36*	0.12**	0.7	52.03	52.77
	C3	0.09*	0.08**	0.33**	0.19*	0.07*	0.58	55..37	38.07
BYP	C1	2.13**	0.42*	1.66*	4.25*	0.07**	2.56	27.78	27.77
	C2	1.55**	0.26*	1.04*	3.11**	0.11**	2.98	24.46	22.76
	C3	1.62**	0.25*	1.02*	3.24**	0.12**	3.18	23.28	19.36
SYP	C1	0.35**	0.06*	0.23*	0.69**	0.01*	3.06	24.45	30.35
	C2	0.17**	0.02*	0.07*	0.34**	0.03*	4.65	16.62	15.10
	C3	0.12**	0.02*	0.07*	0.25**	0.04*	3.7	19.05	10.16
HI	C1	0.66**	0.11*	0.45*	1.32**	0.15**	2.91	23.54	21.15
	C2	0.40**	0.06*	0.24*	0.79**	0.07*	3.32	21.58	14.06
	C3	0.97**	0.13*	0.51*	1.94**	0.13**	2.58	19.64	14.61

* refers to significance at p <0.05 and ** refers to p <0.01

σ^2mL = Mean sum of squares due to interaction in sets; σ^2m = Mean sum of squares due to males in sets; σ^2D = Additive genetic variance;σ^2H = Dominance genetic variance; σ^2E = Error variance; DD = Average degree of dominance; h^2NS = Narrow sense heritability and GA = Genetic advance

by Singh et al. (2018) using diallel analysis; Khodambashi et al. (2012) using generation mean analysis and Kumar and Srivastava (2007) using Line X Tester analysis. Hundred seed weight was the only attribute that showed a preponderance of additive gene action in all three crosses with an average degree of dominance of less than one indicating partial dominance or incomplete dominance. The genetic variability particularly of an additive nature is released in biparental mating as a result of forced recombination resulting in the alteration of linkage disequilibrium (Chandrakant et al. 2015). Abbo et al. (1991) investigated the genetics of seed weight in crosses between the cultivated lentil *L. culinaris* and the wild species *L, orientalis* and *L. ervoides*. They discovered that seed weight is under polygenic control with partial dominance of low seed-weight alleles. The preponderance of additive variance for 100-seed weight in lentils was also reported earlier (Kumar and Srivastava 2007; Tahir et al. 1995; Chauhan and Singh 1995) using diallel analysis. Contrasting results were obtained by Kumar et al. (1996) in lentils as they discovered a higher value of GCA variance than SCA variance for traits days to first flower, plant height, primary branches/plant, and seeds/pod, indicating predominance of additive gene action. They also discovered that gene action is primarily nonadditive for 100-seed weight which contradicts the current experiment's results.

In the present investigation, high narrow sense heritability followed by a high to moderate level of genetic advance was observed for traits viz., 100 seed weight, number of primary branches per plant, number of secondary branches per plant, plant height (cm), number of pods per plant and seed diameter (mm) in all three crosses (Table 5). These findings indicated the critical role of additive gene action in the expression of these traits. High heritability followed by high genetic advance for these traits in lentils was earlier reported by Vanave et al. (2019); Kumar et al. (2009). Traits biological yield, seed yield, and harvesting index had the lowest values of narrow sense heritability followed by a modest degree of genetic advance, indicating the preponderance of dominant gene action in their expression. Khodambashi et al. (2012) also discovered a low value of narrow sense heritability for these traits in lentils. The lowest value of genetic advance was observed for traits days to 50% flowering and days to maturity, suggesting the presence of overdominance and/or higher influence of environment on the expression of these traits. From the findings of the present investigation, it was clear that traits viz., plant height, number of primary branches per plant, number of secondary branches per plant, number of pods per plant, number of pods per cluster, number of seeds per pod, seed yield per plant, biological yield per plant and Harvest index exhibited a preponderance of overdominance type of gene action, which is associated with heterozygosity that is not fixable. Therefore, selection for these traits will not be effective in early segregating generations and it should be delayed to the later generation when most of the loci become homozygous. However, as dominance variance is the chief cause of heterosis, these characteristics can be improved through heterosis breeding. But, being a self-pollinating crop, heterosis breeding is not widely adopted in lentils. Hybridization followed by selection at later generations is suggested for exploiting dominance gene action. In addition to this, two or more cycles of intermating among the selected segregants might break the undesirable linkages and allow the accumulation of favorable alleles to improve traits of interest. Therefore, breeding methods such as diallel selective mating/biparental mating or recurrent selection can be used for their improvement. Hundred seed weight was the only parameter in which additive variance was greater than dominance variance and also showed the highest heritability in all three crosses. Therefore, preference should be given to pureline selection, mass selection and/or progeny selection for improvement of 100-seed weight.

Supplementary material

Supplementary Tables S1 and S2 and Supplementary Figure 1 are provided, which can be accessed at www.isgpb.org

Authors' contribution

Conceptualization of research (SKV); Designing of the experiments (HD); Contribution of experimental materials (SKV); Execution of field/lab experiments and data collection (HD, HY, AKG, DR); Analysis of data and interpretation (HD,, CB); Preparation of the manuscript (HD, SKV, AKG, CC).

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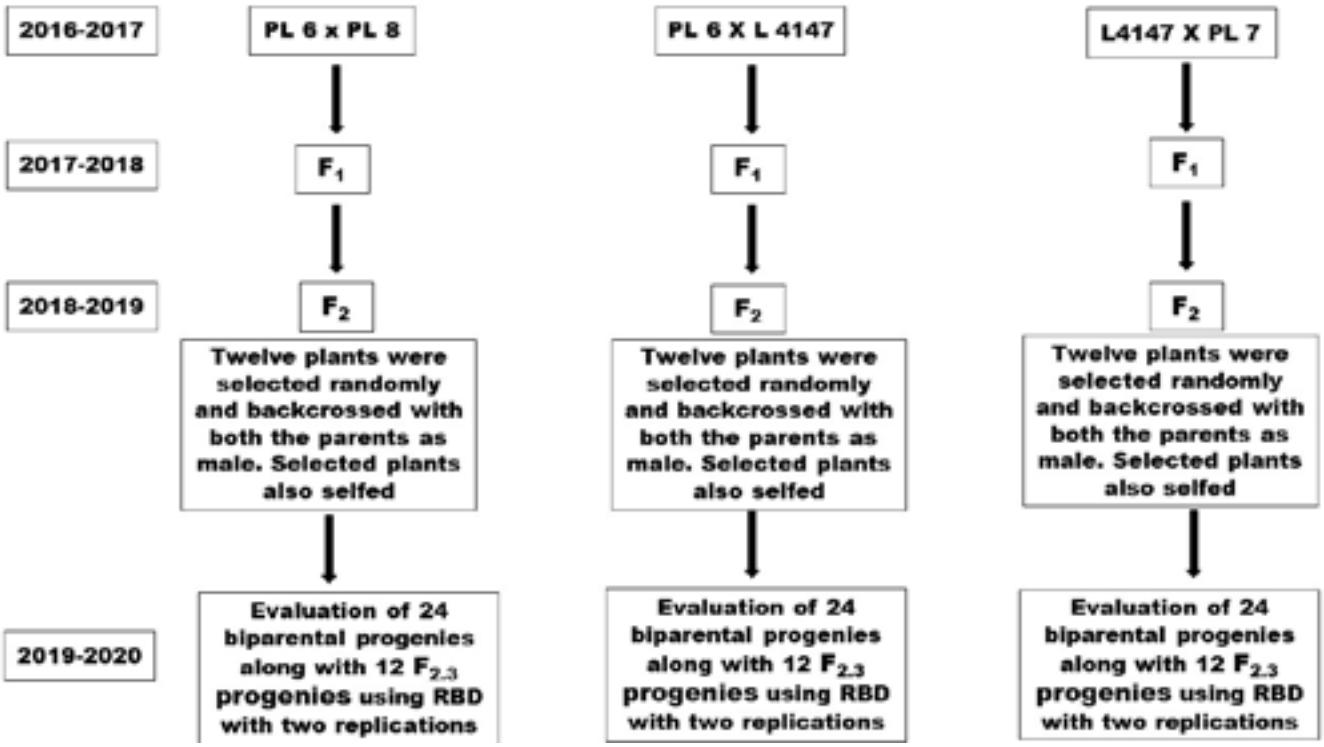
Supplementary Table S1. Parental lentil genotypes, their pedigree and some important characteristics

Genotypes	PL 6	PL 7	PL 8	L 4147
Pedigree	PL-4 x DPL-55	L 4076 x DPL-15	DPL-59 x IPL-105	(L 3875 x PL 4) x PKLV
Seed type	Bold seeded	Bold seeded	Small seeded	Small seed
Days to maturity	115-120	120-125	130-135	135-140
Plant Type	Erect	Semi- erect	Semi-erect	Semi-erect
Foliage Colour	Light green	Dark green	Dark green	Dark Green
Testa Colour	Yellow	Light grey	Grey	Grey
Testa Colour Marking	Non-Mottled	Non-Mottled	Mottled	Non-Mottled



Supplementary Fig. 1. Layout of crossing plan

Supplementary Table S2. ANOVA of North Carolina Design-III for different traits in lentil

Mean Sum Of Squares

		C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3
S.V.	*df*	*DFF*			*DM*			*PH*			*NPB*			*NSB*			*NPP*		
Sets	2	5.10*	4.15	5.58*	9.65**	2.27	33.08**	10.65	2.65	16.19**	0.90**	1.00*	1.65*	12.80**	0.08	1.58	1053.66**	377.33*	19.15
Replications in sets	3	4.10*	18.04**	0.04	4.17*	4.69	11.90	6.40	16.79**	7.88*	1.52	2.43**	0.60	0.69	3.23**	2.17	214.34**	318.50*	27.10
Females in sets	3	8.08**	12.38**	25.85**	133.73**	37.69**	65.56**	20.77**	58.54**	158.63**	9.43**	5.40**	3.44**	6.79*	9.90**	24.33**	1697.41**	2699.33**	1486.77**
Males in sets	9	6.18**	4.88**	4.65**	11.13**	8.69*	13.66**	18.92**	18.80**	16.70**	9.03**	2.23**	1.40**	10.62**	5.59**	4.36**	502.57**	315.70**	228.47**
Interactions in sets	9	11.37**	6.90**	8.19**	22.57**	14.68**	23.91**	35.57**	34.47**	32.23**	17.76**	3.91**	2.02**	22.26**	13.37**	6.39**	951.25**	517.33**	543.69**
Error	21	1.00	1.22	1.44	1.24	2.58	4.28	3.58	2.39	2.39	0.15	0.20	0.41	1.95	0.49	0.97	43.10	71.54	24.01

Mean Sum of Squares

		C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3	C1	C2	C3
S.V.	df	NPC			NSP			SD			HSW			BYP			SYP			HI		
Sets	2	0.46*	0.25	0.46**	0.21*	0.14	0.15	0.29**	0.14	0.26**	0.42**	0.11	0.42*	0.44**	2.39**	0.60*	0.001	0.04	0.48**	0.51	0.49**	2.16**
Replications in sets	3	0.01	0.10	0.01	0.01	0.05	0.14*	0.10*	0.21*	0.10	0.36**	0.38*	0.43**	2.58**	1.57**	0.41*	0.37**	0.21**	0.15*	0.10	0.19	0.62**
Females in sets	3	0.25	0.18	0.25*	0.03	0.13	0.14	0.12**	0.60*	0.30**	0.10*	0.42*	0.71**	0.28*	2.25**	1.07**	0.41**	0.40**	3.21**	0.67*	0.31*	0.93**
Males in sets	9	0.16	0.17	0.16*	0.08	0.08	0.06	0.11**	0.31**	0.16**	0.39**	0.64**	0.40**	1.74**	1.15**	1.14**	0.23**	0.10**	0.10*	0.61**	0.31**	0.63**
Interactions in sets	9	0.15	0.20	0.15*	0.10	0.08	0.08	0.13**	0.36**	0.18**	0.30**	0.48**	0.26**	4.32**	3.22**	3.36**	0.70**	0.36**	0.29**	1.47**	0.86**	2.07**
Error	21	0.12	0.09	0.06	0.05	0.05	0.05	0.02	0.06	0.04	0.03	0.12	0.07	0.07	0.11	0.12	0.01	0.03	0.04	0.15	0.07	0.13

* refers to significance at P<0.05 and ** refers to P<0.01

S.V.=source of variation; df= degree of freedom; C1, C2 and C3 refers to crosses PL 6 x PL 8, PL 6 x L 4147 and L 4147 x PL 7, respectively; DFF= days to 50% flowering; DM= days to maturity; PH= plant height; NPB= number of primary branches; NSB= number of secondary branches; NPP=number of pods per plant ;NPC= number of pods per cluster; NSP= number of seeds per pod; SD= seed diameter; HSW=hundred seed weight; BYP=Biological yield per plant; SYP=Seed yield per plant; HI=Harvesting index