Generation Mean Analysis for Grain Yield and Its Related Traits in Lentil

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ABSTRACT

In order to estimate heritability and gene action for grain yield and its related traits in lentil, six basic generations were evaluated in a randomized complete block design with three replications in a field experiment. Besides seed yield per plant, plant height, pod length, and 100-seed weight, the number of pods per plant, primary branches, clusters per plant, nodes per main stem, secondary branches, and the number of seeds per pod were recorded. Generation mean analysis using A, B, C and joint scaling tests indicated that additive [a], dominance [d] and at least one of the epistatic effect (additive×additive [aa], additive×dominance [ad] and dominance×dominance [dd]) were involved in the inheritance of the studied traits. However, simple additive-dominance model was sufficient only for pod length. Significant dominance [d] and dominance×dominance [dd] interactions with opposite sign indicated duplicate epistasis for all traits except pod length. Narrow-sense heritability was low for seed yield per plant, pod length, number of seeds per pod and 100-seed weight and moderate for other traits. Average dominance ratio was more than unity for seed yield per plant, number of primary and secondary branches, pod length, and 100-seed weight, which showed the high importance of dominance gene effect in control of these traits. Due to the presence of greater non-additive gene effects combined with low narrow-sense heritability, selection for almost all of the studied traits in this cross, especially in early generations, would be complex in conventional methods.

Keywords: Heritability, Lentil, Mean analysis, Seed yield, Yield components.

INTRODUCTION

Lentil (*Lens culinaris* Medik) is the most important food legume crop of rain fed cropping systems in the Near East, traditionally grown in rotation with barley and wheat in low and medium rainfall areas, respectively. Lentil seed is a rich source of protein (up to 28%) for human consumption and its straw is a valued animal feed. In dry years, the income from lentil straw may equal that of seed in many parts of the Near East. Lentil is adapted to less favorable environments and is predominantly winter grown in regions where the annual average rainfall ranges between 300 and 400 mm (Sarker *et al*, 2003).

Seed yield in lentil, same as in all other crops, is due to interaction of many genes with environment, thus, direct selection for it will not be successful. Selection for yield components has been suggested as a solution for further advance in increasing yield. In breeding to increase the inherent yielding potential of a crop plant, the selection criterion may be yield or some of the morphological components of yield. An understanding of the mode of inheritance of the yield components, the correlations among them, and the association between each component with yield is necessary for

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the intelligent choice of breeding procedures for developing high-yielding varieties. One of the best methods for the estimation of genetic parameters is generation mean analysis, in which epistatic effects could also be estimated. Six basic generations variance components can give an accurate information in relating average dominance ratio and inheritance. Thus, these components can complete the derived information from means (Mather and Jinks, 1982; Kearsey and Pooni, 1996). The choice of an efficient breeding procedure depends on the knowledge of the genetic controlling system of the character to be selected (Azizi *et al*, 2006). Aher *et al*. (2006) using generation mean analysis in three crosses from pigeon pea showed that additive component in first cross, dominance component in second cross and both additive and dominance gene effects in third cross were significant for the number of pods per plant.

Hooda *et al*. (2000) observed significant additive gene effects for plant height and 100-seed weight in pigeon pea. Khattak *et al*. (2004) used mean data for six basic generation subjected to joint scaling test for two crosses in mung bean. In the presence of epistasis, a six parameter model was used to detect all types of gene actions. They recorded the duplicate type of non-allelic interactions for number of clusters per plant and 1000-seed weight and complementary type of non-allelic interactions for seed yield per plant in both crosses.

Also, Singh *et al*. (2006) showed that dominance and epistasis effects contribute significantly to heritability of different traits of mung bean. Bhardwaj *et al*. (2005) using generation mean analysis in two crosses of cowpea reported that additive and dominance gene effects were highly significant. In both crosses, additive gene effect for the number of pods per plant and seed yield per plant was greater than the dominance gene effect. They also recorded epistatic gene effects for all studied traits, except for seed yield per plant in both crosses. Aich *et al*. (2007) reported high

heritability for the number of pods per plant and the secondary branches per plant in lentil. The objectives of the present study were: (1) to test suitability of additive - dominance model and (2) to estimate and compare genetic parameters such as gene effects and heritability for some traits of lentil, using six basic generations (P1, P2, F1, F2, Bc1.1 and Bc1.2) of cross between *L-3685* and *Lc74-1-5-1*.

MATERIALS AND METHODS

Quantitative genetics of seed yield and other agronomic characters of lentil were studied using the F_1, F_2, $Bc_{1.1}$ and $Bc_{1.2}$ of a cross between *L-3685* (a small seeded line) as female parent (P_1) and *Lc74-1-5-1* (a bold seeded line) as male parent (P_2) in a complete randomized block design of experiment with three replications at the Shahrekord University of Iran, in 2008-2009.

Plants were cultivated in 2 meters long rows with spacings of 30 and 20 cm between and within the rows, respectively. Four rows of each P_1 and P_2, two rows of F_1, three rows of each $Bc_{1.1}$ and $Bc_{1.2}$ and 12 rows of F_2 plants were cultivated in each replication. Agricultural practices such as irrigation, fertilizer application, and weed control were done uniformly in all blocks.

Data were recorded from single plants with 15 plants of each parent and F_1, 30 plants of each backcross and 60 plants of F_2 in a replicate. The studied characters were seed yield per plant, plant height, 100-seed weight, and pod length as well as the number of pods per plant, seeds per plant, the primary and secondary branches per plant, clusters per plant, nodes per main stem, and the number of seeds per pod,

The observed means of the six generations and their standard errors were used to estimate the mid-parent (m), additive (a) and dominance (d) gene effects using the joint scaling test of Mather and Jinks (1982). The adequacy of the simple additive-dominance model (mean, additive, and

dominance effects) was determined by χ^2 test.

Where the simple model proved to be inadequate, epistasis additive×additive [aa], additive×dominance [ad] and dominance×dominance [dd] were added to the model, as proposed by Mather and Jinks (1982). The significance of genetic parameters (m, [a], [d], [aa], [ad] and [dd]) were tested using *t*-test. In the complete six-parameter model, chi-square adequacy test was not possible, because the degrees of freedom was reduced to zero. In this situation, non-significant terms were eliminated from the full model to generate degrees of freedom for model adequacy χ^2 tests. Ideally, a satisfactory model would produce a non-significant χ^2 value whilst having each component significantly different from zero.

The generation variances were fitted to a model including additive (V_A), dominance (V_D), environmental (V_E) and additive-dominance (V_{AD}) variance components (Kearsey and Pooni, 1996). Variance components were estimated according to Kearsey and Pooni (1996). Narrow sense heritability was estimated by dividing the additive genetic variance (V_A) with the F_2 variance. The average dominance ratio for the characters was calculated as the square root of the ratio of $4V_D$ over $2V_A$. Statistical analysis was done using computer software MINITAB version 14 (Minitab, 2005)

RESULTS

The *Lc74-1-5-1* (P$_2$) mean was greater than the *L3685* (P$_1$) mean for most of the traits (Table 1). The F_1 mean was greater than mean of both parents only for the number of seeds per pod. F$_2$ means for most traits were in the range of the parents mean. Back cross means of the F_1 to the superior parent (P$_2$) showed higher values for most traits compared with back cross means to the inferior parent (P$_1$).

The simple additive-dominance model to generation means showed the three terms (m, [a] and [d]) to be significant for all characters, except the additive component of 100-seed weight (Table 2). However, χ^2 test showed that the simple additive-dominance model fitted only the pod length. Hence, epistatic interactions are involved in genetic control of the other studied traits in this family. Using joint scaling tests, Mittal and Bhardwaj (2008) revealed the presence of epistasis for pods per plant, pods per cluster, 100-seed weight, and seed yield per plant in cowpea. The model with conceding gene interactions showed that although additive effects ([a]) for all traits, except 100-seed weight, were significant, the dominance ([d]) and dominance×dominance ([dd]) interaction appropriated the larger values. Dominance effects were negative for all traits except pod length and the number of seeds per pod.

Estimates of the six-parameter model, including interactions followed by the progressive elimination of non-significant components, showed that seed yield per plant was most effectively described by a model with additive, dominance, additive×additive and dominance×dominance interaction terms (Table 3). A similar model was also suitable for the number of clusters per plant and nodes per main stem.

Plant height, number of pods per plant and number of seeds per plant showed similar patterns, requiring [a], [d] and [dd] components for a good fit. Also, model with [d], [ad] and [dd] components was suitable for 100-seed weight. The number of primary and secondary branches showed similar patterns, including six parameters (m, [a], [d], [aa], [ad] and [dd]). Although in estimating the six parameters the degree of freedom for χ^2 will be zero and testing becomes impossible, but, sincec χ^2 value was almost zero, a six parameter model could be suitable for these two traits.

The results of the estimates for the variance model, narrow sense heritability values, and the average dominance ratio are

611

Table 1. Means and standard errors of the lentil characters for P_1 (L3685), P_2 (LC74-1-5-1), their F_1, F_2, BC_1 (F$_1$ × P$_1$) and BC_2 (F$_1$ × P$_2$).

Character	P_1	P_2	F_1	F_2	BC_1	BC_2
SY[a]	10.96±0.77	13.35±0.83	7.24±0.64	7.16±0.49	4.18±0.79	6.08±0.91
PH[b]	30.7±0.78	32.3±0.79	29.4±0.59	28.6±0.52	26.2±0.71	27.4±0.89
NOP[c]	280.2±14.4	544.7±20.1	286.6±17.1	259.6±16.8	184.4±22.9	259.1±27. 9
NOS[d]	501.9±26.7	851.8±32.6	516.1±29.6	450.9±29.3	329.2±40.2	454.1±50.1
NOPB[e]	12.93±0.38	17.80±0.41	16.17±0.33	15.15±0.34	14.03±0.55	13.9±0.49
NOC[f]	179.4±10.6	356.8±14.4	188.4±10.9	184.5±11.0	118.4±14.3	166.6±19.8
PL[g]	10.93±0.10	11.65±0.10	11.64±0.09	11.47±0.09	11.40±0.15	11.88±0.16
NON[h]	21.67±0.39	25.13±0.48	22.45±0.39	21.82±0.34	20.63±0.54	20.81±0.48
NOSB[i]	44.26±2.11	87.26±1.79	60.58±1.6	49.92±1.77	39.44±2.64	41.78±2.75
NOSP[j]	1.79±0.01	1.56±0.01	1.80±0.01	1.74±0.01	1.799±0.02	1.75±0.02
100 SW[k]	2.23±0.06	2.18±0.06	1.88±0.05	1.63±0.04	1.37±0.07	1.561±0.08

[a] Seed yield per plant (g); [b] Plant height (cm); [c] Number of pods per plant; [d] Number of seeds per plant; [e] Number of primary branches; [f] Number of clusters per plant; [g] Pod length (mm); [h] Number of nodes per main stem; [i] Number of secondary branches; [j] Number of seeds per pod, [k] 100-seed weight (g).

Table 2. Estimates of genetic parameters based on three parameters model (m, [a], [d]) , χ^2 and A, B, C scaling test using six generations of the cross *L3685×Lc74-1-5-1* for agronomic characters in lentil.

	Parameters				Scaling testes		
characters	m	[a]	[d]	χ^2	A	B	C
SY[a]	9.48±0.49**	-1.26±0.51*	-4.48±0.8**	36.87**	-9.18**	-7.63**	-10.06**
PH[b]	30.08±0.48**	-1.10±0.49*	-1.77±0.81*	31.94**	-8.07**	-6.92**	-8.45**
NOP[c]	380.1±11.42**	-120.6±11.6**	-143.0±20.5**	48.5**	-204.9**	-310.6**	-379.8**
NOS[d]	627.9±19.54**	-167.8±19.9**	-190.1±35.43**	40.54**	-367.8**	-448.7**	-614.3**
NOPB[e]	14.88±0.25**	-2.035±0.26**	0.82±0.4*	30.85**	-1.05ns	-6.21**	-2.63ns
NOC[f]	246.5±8.1**	-83.39±8.37**	-85.7±13.9**	39.57**	-135.2**	-201.8**	-182.9**
PL[g]	11.31±0.06**	-0.37±0.071**	0.37±0.11**	1.65ns	0.184ns	0.41ns	0.25ns
NON[h]	22.68±0.28**	-1.33±0.28**	-1.02±0.49*	30.66**	-2.93*	-5.83**	-4.77**
NOSB[i]	60.22±1.26**	-20.29±1.29**	-7.53±2.11**	138.8**	-25.26**	-63.02**	-52.56**
NOSP[j]	1.68±0.01**	0.11±0.01**	0130±0.014**	11.67**	-0.13ns	0.148*	0.015ns
SW[k]	1.99±0.038**	-0.03±0.04ns	-0.35±0.07**	127.1**	-1.42**	-0.99**	-1.75**

Ns; * and **, Non significant, significant at 5% and 1% level, respectively.
[a] Seed yield per plant (g); [b] Plant height (cm); [c] Number of pods per plant; [d] Number of seeds per plant; [e] Number of primary branches; [f] Number of clusters per plant; [g] Pod length (mm); [h] Number of nodes per main stem; [i] Number of secondary branches; [j] Number of seeds per pod, [k] 100-seed weight (g).

presented in table 4. The average dominance ratio was more than unity for seed yield per plant (SY), number of primary (NOPB) and secondary (NOSB) branches, pod length (PL) and 100-seed weight (100 SW), which showed the importance of the dominance gene effects that is in agreement with low narrow sense heritability for these traits (Table 4). The narrow sense heritability estimates for the

Table 3. Estimates of gene effects with standard errors and χ^2 values of the fitted model for studied traits in lentil cross (L3685×Lc74-1-5-1).

characters	m	[a]	[d]	[aa]	[ad]	[dd]	χ^2
SY[a]	20.45±3.17**	-1.32±0.52*	-39.96±8.43**	-8.29±3.12*	—	26.75±5.47**	0.277[ns]
PH[b]	31.52±0.56**	-0.99±0.50*	-13.18±2.34**	—	—	11.59±2.23**	5.026[ns]
NOP[c]	410.87±12.31**	-127.36±11.70**	-544.88±63.25**	—	—	432.30±46.34**	3.354[ns]
NOS[d]	676.31±21.02**	-172.09±19.98**	-840.95±110.07**	—	—	700.11±112.09**	1.534[ns]
NOPB[e]	19.99±2.05**	-2.43±0.28**	-15.56±5.32**	—	5.15±1.59**	11.88±3.39**	1.10[-7ns]
NOC[f]	402.69±46.58**	-84.77±8.42**	-661.33±167.30**	-135.72±64.17*	—	452.10±106.56**	1.638[ns]
PL[g]	11.31±0.07**	-0.37±0.07**	0.36±0.12**	—	—	—	1.65[ns]
NON[h]	27.63±2.01**	-1.50±0.29**	-18.17±5.20**	-4.27±1.98*	—	13.23±3.33**	3.387[ns]
NOSB[i]	101.49±10.52**	-21.50±1.38**	-164.88±27.31**	-35.72±10.42**	37.76±8.12**	124.01±17.36**	4.10[-7ns]
NOSP[j]	1.68±0.01**	0.11±0.01**	0.22±0.05**	—	-0.12±0.06*	-0.09±0.05[ns]	3.709[ns]
100 SW[k]	2.20±0.04**	—	-2.30±0.19**	—	-0.45±0.21*	2.03±0.19**	5.83[ns]

ns, * and **: non significant, significant at 5% and 1% level, respectively.
[a] Seed yield per plant (g); [b] Plant height (cm); [c] Number of pods per plant; [d] Number of seeds per plant; [e] Number of primary branches; [f] Number of clusters per plant; [g] Pod length (mm); [h] Number of nodes per main stem; [i] Number of secondary branches; [j] Number of seeds per pod, [k] 100-seed weight (g).

number of pods per plant (NOP), number of seeds per plant (NOS) and number of seeds per pod (NOSP) were high and equal to 56.77, 54.08 and 70.9, respectively.

DISCUSSION

In this study, in addition to additive gene effects, [d] and [dd] gene effects had high contributions in controlling the studied traits. Gene interaction is considered to be complementary when the [d] and [dd] estimates have the same signs and to be duplicating when the signs differ (Mather and Jinks, 1982). Gene interactions in this study were of duplicate type for all traits except pod length. Khattak *et al.* (2004), who studied six basic generations from one cross in mung bean, showed that duplicate type of non-allelic interactions exist for the number of clusters per plant. Duplicate type of non-allelic interactions were also reported for plant height and th number of tillers in wheat (Dashti *et al.*, 2010); for plant height in maize (Azizi *et al.*, 2006), and for plant height, number of primary and secondary branches, pod per plant, seed per pod, pod length, 100 seed weight and yield per plant in mungbean (Singh et al., 2007). Positive or negative form of additive×additive [aa] interaction show association and dispersion of alleles in parents, respectively. Therefore, negative and significant values of [aa] in this study showed alleles dispersion in parents for seed yield per plant, number of clusters per plant, number of nodes per main stem, and number of primary and secondary branches. The sign of dominance [d] gene effects and dominance×dominance [dd] interaction show dominance direct and unidirectional or ambidirectional dominant, respectively. Negative sign of dominance [d] gene effect show that reductive alleles involving dominant phenotype otherwise increasing alleles include dominant phenotype. Also negative sign of dominance×dominance [dd] interaction show ambidirectional dominant. In the present study, for most traits, it was observed that dominance direct was unidirectional dominant and reductive alleles were involved in dominant phenotype.

The difficulty exists in describing generation mean analysis when balance effects of all loci are

Table 4. Estimates of additive (V$_A$), dominance (V$_D$), additive-dominance (V$_{AD}$) and environmental (V$_E$) variances; narrow-sense heritability (h_n^2) and average dominance ratio (DD) for the lentil characters in cross *L3685×Lc74-1-5-1*.

characters	V_A	V_D	V_{AD}	V_E	h_n^2	DD
SY [a]	2.55	2.89	2.04	9.78	16.74	1.50
PH [b]	5.93	1.65	3.02	9.20	35.34	0.74
NOP [c]	9838.33	2079.98	2376.05	5410.30	56.77	0.65
NOS [d]	26853.19	9841.11	8476.69	15873.86	51.08	0.86
NOPB [e]	2.79	1.90	-0.67	2.53	38.74	1.16
NOC [f]	3634.20	1178.60	1867.21	2567.20	49.24	0.80
PL [g]	0.10	0.28	0.01	0.18	17.90	2.35
NON [h]	3.27	0.52	-0.66	3.30	46.20	0.56
NOSB [i]	78.14	53.14	6.35	60.80	40.68	1.17
NOSP [j]	0.01	0.05	0.01	0.0002	70.90	0.36
100 SW [k]	0.02	0.04	0.02	0.059	20.77	1.70

[a] Seed yield per plant (g); [b] Plant height (cm); [c] Number of pods per plant; [d] Number of seeds per plant; [e] Number of primary branches; [f] Number of clusters per plant; [g] Pod length (mm); [h] Number of nodes per main stem; [i] Number of secondary branches; [j] Number of seeds per pod, [k] 100-seed weight (g).

segregating. Thus, additive gene effects, or interaction effects relating to additive gene effects, are subjected to the degree of increasing gene dispersion of traits between parents, whilst dominance gene effect is pure multiple of dominance direct in each locus. Therefore, additive gene effect may be little because of gene dispersion and also dominance gene effect can be little because of ambidirectional dominant. But, genetic variances are mean squares of each locus effects and are not affected by gene dispersion and dominance direct. Thus, data of generation variances can be used to complete genetic information. In relation with generations variance, epistasis only affect transgressive segregating generations variances, therefore, because of the presence of epistatic effects, the estimate of V_A and V_D components would not be unbias, consequently, heritability will also be affect by epistasis.

Beside joint scaling test, scaling test A, B and C showed that simple additive- dominant model was not suitable for the studied traits, except pod length (Table 2). Considering the expected values for scaling test A, B, C as explained by Kearsey and Pooni (1996), negative and significant values of these tests for traits such as seed yield per plant, plant height, and 100 seed weight as well as the number of pods per plant, seeds per plant, clusters per plant, nodes per

main stem, and the number of secondary branches indicated the importance of epestatic effects [aa] and [dd] in the control of these traits. Significance of only scaling test B for the number of primary branches and seeds per pod could be considered as an indicator of the important role of epistatic effect [ad] in the control of these two traits.

In this study, estimates of V_A and V_D components of all traits, except pod length, were not free of bias, because of the presence of epistatic gene effects. Under such circumstances, V_A is affected by the presence of [aa] and [ad]. The presence of [aa] often inflates the variance of F$_2$ and its subsequent generations, while [ad] increases it when positive and decreases it when negative. V$_D$ is also affected by [ad] and [dd] when genes interact and [dd] increases the variance of F$_2$ when having the same sign with [d] and decreases it when it has the opposite sign (Mather and Jinks, 1982). Epistasis of the [aa] type observed in this experiment could be used in the breeding programme with the additive component since it is fixable.

Nevertheless, the [ad] and [dd] types of interaction may not be of any advantage in developing inbred varieties of lentil as these terms are not fixable by selection. The complication created by these interactions may be averted by delaying selection to later

generations with increased homozygosity, where additive and additive×additive variances are prevailing. High values of narrow-sense heritability estimated for the number of pods per plant (NOP), seeds per plant (NOS) and seeds per pod (NOSP) indicate that selection for these three yield components is likely to be successful. Because the low narrow sense heritability was estimated for pod length and 100-seed weight, it is apparent that selection for these traits will be difficult and high environmental influence will be a problem.

For selection based on yield components to be effective in increasing yield, it is important that the components should be highly heritable and strongly and positively correlated with yield. The number of pods and seed yield per plant, which showed relatively high narrow-sense heritability estimates (60.5 and 41.9% respectively), were considered the best predictors of seed yield in cowpea (Ojo et al., 2009). In studies of Gangele and Rao (2005) on lentil genotypes and Arshad *et al.* (2002) on cowpea, genotypes reported low heritability for pod length and seed yield per plant, respectively. Also, Bicer and Sakar (2004), Singh and Singh (2004), and Khan *et al.* (2006), in lentil, Saleem *et al.* (2002) in chickpea, and Salgotra and Gupta (2005) in common bean observed high heritability for plant height, 100-seed weight, number of seeds per pod, and seed yield per plant.

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تجزیه میانگین نسل ها برای عملکرد و صفات وابسته به آن در عدس

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چکیده

به منظور برآورد میزان وراثت پذیری و تعیین نحوهٔ عمل ژن برای عملکرد دانه و صفات مرتبط در عدس، شش نسل پایه شامل (L3685)P_1، (Lc74-1-5-1)P_2، F_1، F_2، $Bc_{1.1}$ و $Bc_{1.2}$ در قالب طرح بلوک های کامل تصادفی با سه تکرار در مزرعه کشت و برای صفات عملکرد دانه در بوته، ارتفاع بوته، تعداد غلاف در بوته، تعداد دانه دربوته، تعداد دانه درغلاف، تعداد شاخه اولیه و ثانویه در بوته، طول غلاف، تعداد گره در ساقه اصلی، و وزن صد دانه مورد بررسی قرار گرفتند. تجزیه میانگین نسل ها با استفاده از آزمون‌های مقیاس A، B، C و توأم نشان داد، اثرات افزایشی [a]، غالبیّت [d]، و حداقل یکی از انواع اپیستازی (آثار متقابل افزایشی در افزایشی [aa]، افزایشی در غالبیّت [ad] و غالبیّت در غالبیّت [dd]) در کنترل ژنتیکی صفات نقش دارند و تنها در مورد طول غلاف مدل ساده افزایشی- غالبیّت ژن‌ها کفایت نمود. معنی‌دار و مخالف بودن علامت پارامترهای غالبیّت [d] و اثر متقابل غالبیّت در غالبیّت [dd] دال بر وجود اپیستازی از نوع مضاعف برای کلیّهٔ صفات به غیر از طول غلاف می باشد. مقدار توارث پذیری خصوصی برای صفات عملکرد دانه در بوته، طول غلاف، تعداد دانه در غلاف و وزن صد دانه پایین (۳۸/۷۴– ۱۶/۷۴ درصد) و برای سایر صفات مورد مطالعه متوسط (۷۰/۹۰– ۴۰/۶۸ درصد) بود. متوسط نسبت غالبیّت برای صفات عملکرد دانه در بوته، تعداد شاخهٔ اولیه و ثانویّه، طول غلاف و وزن صد دانه بیشتر از یک بود که نشاندهندهٔ اهمیّت آثار غالبیّت برای این صفات است. سهم بالای اثرات غیر افزایشی به همراه وراثت پذیری خصوصی نسبتاً پایین صفات در این تلاقی عمل انتخاب، بویژه در نسل های اولیه تفرق را به روش های مرسوم اصلاحی پیچیده می نماید.