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A Survey of Lettuce (Lactuca sativa L.) floweringtimeduringfallcultivationby the use of Generation Mean Analysis Method

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Abstract: *To study the heredity of lettuceflowering time, the crossing of the selected lines of Shiraz lettuce local mass, as the maternal parent, and the local masses of Zeereae lettuce and Black lettuce, as the paternal parent (which varied in terms of flowering time), the* BC_1P_2, BC_1P_1, F_2, *and* F_1 *generations were prepared through two different crosses. The transplant of each generationwas obtained from each crossand was used for the fallplanting, using two separate experiments, which were carried out in the form of the complete randomized block design with three replications and the flowering time, head weight, and the number of leaves were recorded in order to estimate the genetic parameters and the heredity of the flowering time using the generation mean analyses method. The assessment of the planting time revealed that the number of days to the first flowering was 164, 125.5, and 109 days in the late bolting,early bolting, and hybrid lines, respectively. This finding reflects the over-dominance effect. The average head weight in the latebolting (572 gr) was more than the early bolting (393 gr) line. The results of the generation mean analysis indicated the inadequacy of the dominance in terms of the additive model traits and showed the involvement of other factors such as epistasis in controlling the traits. The additive effect and dominance were significant, whereas the dominance effect was more effective. In addition, the additive × additive epistasis effectsand the dominance × dominance effect also affected the traits. To determine the number of factors influencing the planting time, the rule of segregationwas applied to the F2 generation, and the involvement of two genes in the bolting time was confirmed. In general, since the expected performance of the latebolting lines were not achieved unlike the early bolting time despite the delayed bolting, it could be concluded that the late bolting genotypes should be cultivated during spring and summer to secure the maximum performance. Since late bolting is highly correlated with important traits including the number of leaves and head weight, the selected latebolting genotypes are expected to demonstrate considerable potential for the expression of these traits in the segregating populations.*
Keywords: *bolting, bolting stimuli, lettuce, generation mean analysis*

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I. Introduction

Lettuce (*Lactuca sativa* L.) belongs to the Asteraceae family. It is a self-fertile annual plant with 2n=2x=18 chromosomes (Ryder, 1986). The global production of lettuce from an area of one million hectares equals 22 million tons, and by producing 550,000 tons of lettuce, Iran has the fifth rank in this field in the world. In most plants, the transition from the vegetative phase to the reproductive phase is controlled by the environment and genetics (Corbesier&Coupland, 2005). Heat and daytime are among the factors invoking bolting (untimely bolting) and bolting in lettuce. The lettuce stem, which grows after the onset of the reproductive phase, carries capitols (panicle). In general, bolting of leaf vegetable is unwanted, because it not only reduces the efficiency of the plant, but also reduces the product quality and its popularity in the market due to the production of certain substances. When bolting occurs in lettuce, some secondary metabolites such as Laktin and DeoxyLaktin (which are produced to protect the florets from pests) are secreted, cause the bitter taste of the plant and reduce its marketability.

The first research on the genetics of bolting in lettuce and its properties was conducted by Bremer (1931) through the introduction of a gene that had dominance effects, which leads to daytime bolting. He used the letter T to show this gene. In the regressive state this gene has neutral day phenotypes. In 1983, anearlybolting control gene was introduced by Ryder (1983) and shortly after a second gene involved in the earlybolting control was introduced (Ryder, 1988). These two genes were named $Ef_{-1}ef_{-1}$ and $Ef_{-2}ef_{-2}$, respectively. This trait is correlated with the photoperiod and all of the genotypes show a slower flowering process under short day conditions as compared to the long day conditions.

Silva et al. (1999) selected two early and late bolting varieties as the parents. Their investigations revealed that more than one gene location was involved in the controlling of bolting time. The analysis of the dominance-additive model proved the adequacy of the model and reflected the lack of epistasis in connection with bolting. The additive effect affected the bolting trait more than the dominance effect, and the mean dominance degree, in the two crosses, was 0.58 and 0.38. Broad-sense heritability levels were 0.74% and 82%, while narrow-sense heritability levels were 49% and 48%. The F1 results showed the mean value of the parents in terms of the number of days to the first flower in both crosses. Transgressedsegregationwas observed with regard to early and late bolting in both crosses. This finding suggests that more than one locus is involved in the development of this trait. The generation mean analysis approved the dominance-additive model. The present research was an attempt to conduct a genetic study on the bolting time and its relationship with the plant performance. The ultimate goal of this research was to incorporate the results in the lettuce corrective programs.

II. Materials and Methods

The seeds of the BC_1-P_1, BC_1-P_2, F_2, and F_1 generations obtained from the first cross (C_1) including line no. 3 (selected from the Zeereae lettuce mass), as the paternal parent, and line no. 9 (selected from the Shirazi mass), as the maternal parents, were prepared with a 30-day bolting interval. The seeds of these generations were also selected from the second cross (C_2) including line no. 2 (selected from the Black lettuce mass), as the paternal parent, and line no. 11 (selected from the Shirazi mass), as the maternal parent with a 29-day bolting interval. The seeds were planted in a greenhouse with 16 hours of lighting and 8 hours of darkness at the nighttime and daytime temperatures of 15 and 25 $^{\circ}C$, respectively. The colors of the maternal parent seed and paternal parent seed were white and black in both crosses, respectively, so that the seed resulted from self-fertility and crossing could be distinguished. First, the seeds of the generations resulted from crossing were transplanted along with the parents in the greenhouse. In the late August 2015, the transplants were planted throughout two separate experiments in the form of a complete randomized block design through 3replications in the 400-ha farm of the Seed and Plant Improvement Institute. The distance between the planting lines was 30 cm and the seeds were planted on 25-cm lines. In each replication, 2 five-meter lines of the parents and F_1 generation, four lines of backcrosses, and ten lines of the F_2 generation were cultivated. Moreover, 100 kg/ha of the urea fertilizer and 250 kg/ha of the ammonium phosphate fertilizer were used during cultivation, and the 3 twenty fertilizer was administered every week by spraying its solution. Upon opened the first flower, the stem was removed and the head weight, the number ofleaves, and the bolting time (days to the first flower opening) were recorded. The weighted analysis of variance of the generations was carried out and the generation means analysis and the generation analysis of variance were performed by the use of the Excel functions. The adequacy of the dominance-additive model was examined through a scaling test and the generation mean analysis was conducted using Cavalli's method (1952).

First, the m, [h], and [d] parameters of the traits of concern were estimated. Afterwards, the estimates were used to calculate the expected mean values. In the end, the chisquare (X^2) test method was utilized to compare the observed and expected mean values. Given the inadequacy of the dominance-additive model, the six-parameter [l], [j], [i], [h], [d], m Jinks and Jones (1958) model and Cavalli's five-parameter model were used to obtain the estimates. The t test method was also employed to examine the significance of the deviation of the estimated parameters from zero. To determine the number of the effective factors, the segregation of the bolting trait was analyzed in F_2, and the expected number was calculated with the 1:3, 1:15, and 1:63 ratios for one, two, and three genes, respectively. The results were compared to the observations using the chisquare test method.

III. Results and Discussion

The results of the weighted analysis of variance indicated that in both crosses there was a significant difference between the generations of concern in terms of the traits. This significant difference between the generations most probably reflects the existence of a genetic variation, and thus the genetic parameters explaining these trait changes can be estimated using the generation mean analysis of the generations. Table (1) presents the mean traits of the parents and the generations resulting from the 9x3 (C_1) cross and the 11x2 (C_2) cross. As regards the bolting trait, the paternal parent (2 and 3) was more latebolting than the maternal parent (9 and 11) in both crosses and had a larger head weight mean. The mean days to the first flowering of the F_1were fewer than the early bolting parent, which indicates that early bolting has an over-dominance effect. Moreover, in the heterozygote, the expression of this gene increases and thus the F_1 are more early bolting than the parents and they change phase more quickly. In addition, through the transition from the vegetative phase to the reproductive phase, the production and growth of leaves as well as the increase in the head weight stopped. These findings are not in line with the findings reported by Ryder and Miligan (2005), who stated that the genes controlling the bolting time are controlled by the genes that have complete and incomplete dominance effects. However, the present research findings comply with the findings by Kim and Ryder (2003) who stated that early bolting is in an over-dominance state in relation to late bolting.

Table (1): The mean and standard deviation of the traits of the parents and the generations resulting from the 9x3 (C_1) and 11x2 (C_2) crosses

Trait	cross	P_1	P_2	F_1	F_2	BC_1P1	BC_1P2
Head Weight	C1	586.38±7.37	385.52±7.02	365.18±6.90	401.58±10.38	436.59±8.75	340.85±8.73
	C2	559.35±7.33	399.84±7.17	367.85±7.70	439.76±10.57	501.23±8.63	415.56±9.16
leaf num.	C1	37.45±1.15	30.12±1.29	25.96±1.14	32.79±0.97	34.75±1.30	.73±1.06
	C2	37.85±1.20	28.35±1.24	25.46±1.01	28.94±0.84	34.87±1.20	27.54±0.92
days to first flower	C1	169.85±0.97	129.46±0.87	108.60±0.82	132.45±1.01	129.54±1.56	107.65±1.41
	C2	159.95±0.92	122.32±0.82	110.28±0.78	139.87±0.97	129.45±1.51	108.57±1.30

The results of the scaling test carried out to test the adequacy of the dominance-additive model are listed in Table (2). As seen, the dominance-additive model lacks adequacy in all of the traits and other factors such as epistasis contribute to the control of the studied traits. As indicated in Table (3), for a more precise analysis of the adequacy of the dominance-additive model, a generation mean analysis was carried out using Cavalli's (1952) three-parameter model and the adequacy of the model was tested using the chi square test method. As seen, the fitness of the model was not confirmed using the three-parameter model and the three-parameter fitness of the traits was rejected. In addition, the inadequacy of the dominance-additive model and the existence of epistasis were confirmed.

Table (2): The results of the scaling test on the traits of concern in both crosses of lettuce

Trait	**cross**	**A**	**B**	**C**
Head Weight	**C_1**	**78.38±5.64****	**-68.99±5.45****	**-95.93±7.89***
	C_2	**75.26±1.31****	**63.43±4.95****	**64.15±6.93^{ns}**
leaf num.	**C_1**	**6.09±0.49***	**7.38±0.53****	**11.67±0.81***
	C_2	**6.43±2.17***	**1.27±2.19^{ns}**	**-1.36±3.07^{ns}**
days to first flower	**C_1**	**-19.37±1.65****	**-22.76±1.59****	**13.29±2.54****
	C_2	**-11.33±2.07****	**-15.46±2.12****	**56.65±3.12****

*** A, B, C are the test functions**

Table (3): The mean values and the genetic components estimated for the traits of concern in both of the lettuce crosses – the three parameter model

Trait	**cross**	**[m]**	**[d]**	**[h]**	**X^2**
Estimate Head Weight	**C_1**	**476.55±1.45****	**99.43±1.46****	**-128.44±2.66****	**25.28****
	C_2	**487.07±0.54****	**80.79±0.55****	**-101.57± 0.91****	**20.33****
Estimate leaf num.	**C_1**	**35.15±0.55****	**3.28±0.55****	**-6.97±1.01****	**11.72***
	C_2	**33.46±0.54****	**5.22±0.0.55****	**-7.39±0.98****	**7.98***
days to first flower	**C_1**	**148.79±0.49****	**20.43±0.47****	**-41.63±0.93****	**106.98****
	C_2	**142.22±0.53****	**19.27±0.53****	**-30.26±0.96****	**249.53****

m: mean; [d]: additive effects; [h]: dominance effects (significant at the $1\%\alpha$ and $5\%\alpha$ levels and ns insignificant)

In Table (4), the [l], [j], [i], [h], [d], and m parameters were estimated using Jinks and Jones (1958) six-parameter model. All of the parameters of the six-parameter model, except for the dominance x additive effect [j] are significant. Since six generations were used to estimate the parameters, only five parameters can be fit by the chi square test with a single degree of freedom (SDOF). Hence, the [j] parameter was ruled out and five parameters were re-estimated using Cavalli's method (Table 5). A chi square test was also carried out and revealed that the estimates obtained using the five-parameter model fitted the observed data, and the hypothesis about the existence of epistasis was approved in addition to the dominance and additive effects. A significant additive effect was observed on the head weight, the number of leaves, and the number of days to the first flower, but the dominance effect had a larger effect than the additive effect. Considering the resulting degree of dominance it could be concluded that the dominance effects contributed to the controlling of the traits extremely more than the additive effects.

The examination of the number of days to the first flower, the number of leaves and head weight (Table 4) revealed that the factors influencing the phenotypes were the same and followed the same pattern. Seemingly, the terminal meristem stops the leaf generation upon the change of phase, and thereby a bolting stem grows. Hence, through the change of phase, which eventually leads to bolting, the number of the head leaves and the head weight are affected. The difference between the directions of [h] and [l] reflects a dual epistasis, which often reduces the variance of the segregating families (Malhorta et al., 2003).

The variation of the [d] and [i] directions reflects the contradictory nature of the mutual effect on the trait, which adds to the complexity of the genetic analysis and selection. Table (6) presents the variation and the corresponding dominance degree. As seen, all of the traits of concern (except for the number of leafs) the variance of dominance accounts for the maximum variance. The average dominance also suggests that the highest effect on the variation resulted from the over-dominance effect.

Table (4): The estimated mean values and genetic components of the traits under study in the two crosses of lettuce – The six-parameter model

Trait	cross	[m]	[d]	[h]	[i]	[j]	[l]
Estimate Head Weight	C_1	537.39±8.76**	100.44±1.64**	-371.02±23.05**	-51.44±8.6**	-9.39±7.22^{ns}	-198.81±13.19**
	C_2	405.06± 9.60**	79.76 ± 0.56**	176.03 ±24.64*	74.54 ± 9.59**	11.83± 6.96^{ns}	-213.23 ± 15.39**
Estimate leaf num.	C_1	31.99±3.39**	3.67±0.62**	9.25±0.0.9^{ns}	1.8±0.8^{ns}	-1.29±0.98^{ns}	-15.27±0.97^{ns}
	C_2	24.04±3.56**	4.75±0.61**	18.18±3.45^{ns}	9.06±3.51*	-5.16±2.88^{ns}	-16.76±2.05*
days to first flower	C_1	205.08±2.42**	20.19±0.58**	-194.03±6.28**	-55.42±2.34**	3.39±2.02^{ns}	97.55±4.19**
	C_2	224.58±3.52**	18.82±0.59**	-224.53±9.10**	-83.44±3.47**	4.13±0.75^{ns}	110.23±5.86**

M:mean; [d]: additive effects; [h]: dominance effects; [i]: additive x additive effect; [j]: additive x dominance effect; [l]: dominance x dominance effect; [h/d]: mean dominance (significant at the $1\%\alpha$ and $5\%\alpha$ levels and ns insignificant)

Table (5): The estimated mean values and genetic components of the traits under study in the two crosses of lettuce – The five-parameter model

Trait	cross	[m]	[d]	[h]	[i]	[l]	*Chi square* $X^2_{\alpha=0.01,df=1}$	Mean dominance [h\d]
Estimate Head Weight	C1	537.39±7.76**	99.75±4.72**	-371.89±19.25**	-51.42±6.1**	-198.73±13.19**	0.12^{ns}	3.72
	C2	404.44± 12.70**	80.76 ± 0.57**	177.88 ±21.54*	75.14 ± 7.89**	-214.46 ± 12.19**	0.19^{ns}	2.2
Estimate leaf num.	C1	31.99±3.39**	3.67±0.62**	9.25±0.0.9^{ns}	1.8±0.8^{ns}	-15.27±0.97^{ns}	0.4^{ns}	2.78
	C2	24.04±3.56**	4.75±0.61**	18.18±3.45^{ns}	9.06±3.51*	-16.76±2.05*	0.04^{ns}	2.81
days to first flower	C1	205.41±5.58**	20.34±0.62**	-195.04±15.07**	-55.74±5.82**	98.22±9.52**	0.02^{ns}	9.59
	C2	225.03±5.61**	18.99±0.59**	-225.89±14.43**	-83.87±5.57**	111.14±9.12**	3.55^{ns}	11.89

M:mean; [d]: additive effects; [h]: dominance effects; [i]: additive x additive effect; [j]: additive x dominance effect; [l]: dominance x dominance effect; [h/d]: mean dominance (significant at the $1\%\alpha$ and $5\%\alpha$ levels and ns insignificant)

Table (6): Components of the variance and dominance degree of the genes controlling the traits of concern in both of the lettuce crosses

Trait	cross	D	H	E	F	h^2_B	h^2_n	[H/D]^0.5
Estimate Head Weight	C_1	102586.68	-82898.9	4090.31	31.38	88.2	54.1	0.89
	C_2	106564.16	-87181.12	4499.71	-1099.82	87.5	53.8	0.91
Estimate leaf num	C_1	544.53	-332.09	112.32	66.44	88.6	55.1	0.78
	C_2	366.5	-273.41	110.91	70.81	85.23	48.81	0.86
days to first flower	C_1	270.54	523.18	62.43	54.19	92.7	31.6	1.39
	C_2	247.64	487.26	56.11	54.90	92.91	31.31	1.40

D: additive variance; H: dominance variance; E: environmental variance; F: epistasis variance; h2: broad-sense heritability; h2: narrow-sense heritability; [H/D]^0.5 degree of dominance

The narrow-sense heritability is expected to decrease with an increase in the dominance variance and a decrease in the additive variation. As seen, in the case of the traits with a larger share of the variation of the additive variance, the narrow-sense heritability of the trait is higher than the case in which the variance of dominance has a larger share of the variation.

In Table (7), the correlations between the traits suggest that the trend of changes in the number of leaves, the number of the days to the first flower, and the head weight are very similar and strongly correlated.

Table (7): Coefficients of correlation of the generations in terms of the traits of concern in both crosses

trait	cross	Head Weight	Leaf num.	days to first flower
Head Weight	C_1	1		
	C_2	1		
Leaf num.	C_1	0.78	1	
	C_2	0.98	1	
days to first flower	C_1	0.96	0.85	1
	C_2	0.85	0.82	1

C_1: (3x9); C_2(2x11)

To determine the number of factor (genes) contributing to the expression of the number of the days to the first flower (the bolting time) the segregation of the F_2 generation was studied and the expected frequencies of 1, 2, and 3 involved genes were calculated and compared to the observed frequencies of the highly late-bolting genotypes and other genotypes of the F_2 population. The best fit was also selected using the chi square test. The results of both crosses in terms the frequency of the genotypes and transgressed segregation on both sides (more early bolting than an early bolting parent and more late bolting than a late bolding parent) support the hypothesis about the role of two genes in controlling bolting in the genotypes of concern (Fig. 1 and 2).

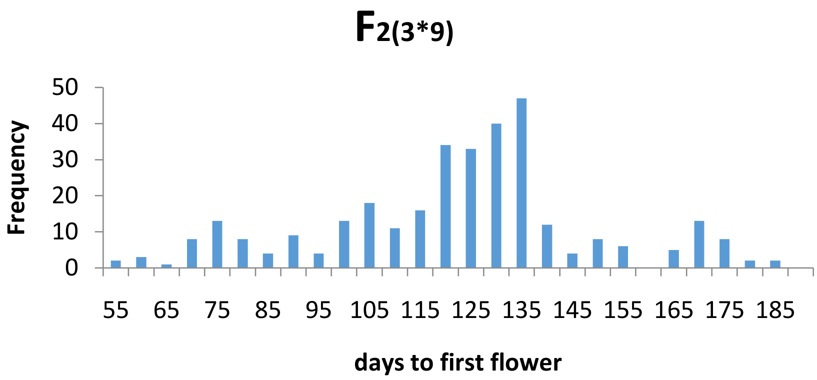

Figure (1): The frequency of the genotypes in the F_2 population in cross one (C_1): 63:1 ratio: for three genes with X2=106.52 and p<0.001; 15:1 ratio: for two genes with X2=3.29 and p=0.04-0.1; and 3:1 ratio: for one gene with X2=45.65 and p=<0.001

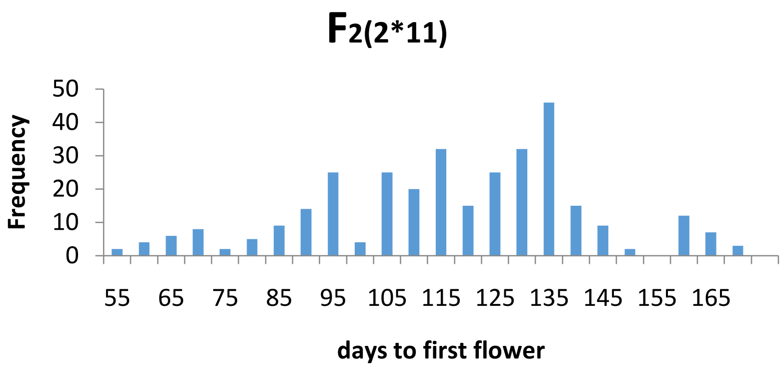

Figure (2): The frequency of the genotypes in the F_2 population in cross one (C_2): 63:1 ratio: for three genes with X2=58.14 and p<0.001; 15:1 ratio: for two genes with X2=0.19 and p=0.04-0.10; and 3:1 ratio: for one gene with X2=56.68 and p=<0.001

IV. Conclusions

Early bolting is one of the problems caused by the global warming and climatic changes. On one hand, the latebolting varieties show less reaction to heat as compared to the early bolting varieties and their bolting time is less affected by higher temperatures. Therefore, the latebolting varieties are recommended for planting. On the other hand, the highly latebolting phenotypes of segregating populations contain the latebolting pure genotype, and therefore the selection of these phenotypes most probably leads to the transfer of the latebolting trait to the next generation. Moreover, since late bolting is highly correlated with the number of leaves and head weight, selection of the latebolting genotypes leads to the selection of genotypes with larger qualitative and quantitative potentials than the other genotypes of the population.

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