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Inheritance of Earliness and Bulb Weight in the Common Onion (Allium cepa L.)

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ABSTRACT

The objective of the present study was to investigate the genetic behaviour of two characters in onions (Allium cepa L.), namely, earliness and bulb weight. Two crosses were made, the first involved the Egyptian cultivars Behairy and Giza 6 Mohassan and the second was between two local inbred lines L 1421 and L 324. Behairy and L 1421 were late in maturity, whereas L 324 was early. Giza 6 Mohassan cultivar was characterized by moderate earliness. With respect to bulb weight, Behairy and L 324 parents showed higher bulb weight than Giza 6 Mohassan and L 1421 parents. Parents, F_1, and F_2 were grown and measurements were recorded. Data were then genetically and statistically analysed.

The F_2 distributions of the first and second cross indicated partial dominance of lateness over earliness. F_2 distributions of both crosses showed some skewness toward lateness but it was significant only in the second cross. It was difficult to draw a certain conclusion concerning the action of genes involved in the inheritance of this character. However, F_1 results of the first cross indicated multiplicative gene action. The results suggested the presence of more than one pair of genes controlling the character. Heritability values ranged from 37.8 to 52.75%. Based on 5% selection intensity, the F_3 mean would be expected to be shifted 4.95-5.47% earlier than the F_2 means in the first and second cross, respectively.

Small bulb weight was overdominant to larger bulb weight. F_2 distributions of both crosses showed positive and highly sinificant skewness. The determination of gene action was difficult in the first cross, but the second cross indicated additive gene action. At least one pair of major genes was found to control the parental differences in bulb weight. High to moderate heritability values were obtained, 77.77 and 48.53% for the first and second cross respectively. Based on 5% selection intensity, the expected genetic gain in F_3 ranged from 50.19–80.35% of the F_2 means for the second and first cross, respectively.

INTRODUCTION

The present studies were carried out to investigate the pattern of inheritance of earliness and bulb weight. Estimates of their heritability values were also determined

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using two open-pollinated cultivars and two local inbred lines. Knowledge of the pattern of inheritance of bulb characters and their heritability values may be useful to the plant breeder in predicting the effectiveness of selection and determining the proper breeding method.

Few intervarietal hybrids in onions produced much larger yields than the parental varieties, as reported by Jones and Davis (5). Many of them are not superior to non-hybrid varieties in yielding ability. Heterosis for bulb weight was not observed in crosses between high yielding male sterile lines and inbred lines of lower vigour, though the value of the better parent was sometimes attained (6). McCollum (8) reported that heritability value for bulb weight is low or zero. Progress in breeding for earliness had been made in Egypt as reported by Ahmed (1). Some lines, that were obtained through single plant selection in local strains, were three weeks earlier than the standard Giza 6 Mohassan cultivar. Orlova (10) made various crosses and found that earliness showed intermediate inheritance. Hosfield *et al.* (4) found that maternal influences were important for yield and maturity.

MATERIAL AND METHODS

Two cultivars, namely Behairy and Giza 6 Mohassan were utilized. In addition two local lines in S_3, namely L 1421 and L 324, that were selected from local strains through single plant selection, were chosen from the available breeding stocks. The behaviour of these cultivars and lines with respect to bulb weight and earliness was as follows:

Cultivar or line	Average bulb weight in grams	Approx. time to maturity in days
Behairy	138.82 ± 2.88	144 (late)
Giza 6M	85.26 ± 2.06	129 (moderate earliness)
L 1421	76.32 ± 3.12	141 (late)
L 324	95.57 ± 2.82	117 (early)

Two crosses were made, the first was a varietal cross (Behairy × Giza 6 M) and the second was between the two lines (L 1421 × L 324). F_1 and F_2 generations were produced. All observations were recorded on plants of parents, F_1, and F_2 seeded in one growing season under Shandaweel conditions. Earliness was determined by recording the number of days from transplanting to the maturity stage of each bulb. After harvesting, the weight of each bulb was recorded.

For each population (P_1, P_2, F_1 and F_2), the mean, variance, and coefficient of variation were calculated to estimate the relative degree of variability in each population. In order to determine the degree of dominance and the nature of gene action the following statistical values were calculated:

$$\text{The expected arithmetic mean of the } F_1 = \frac{\overline{P}_1 + \overline{P}_2}{2}$$

$$\text{The expected arithmetic mean of the } F_2 = \frac{\overline{P}_1 + 2\,\overline{F}_1 + \overline{P}_2}{4}$$

where $\overline{P}_1$ is the observed mean of one parent

$\overline{P}_2$ is the observed mean of the other parent.

$\overline{F}_1$ is the observed mean of the F_1 population.

$$\text{Geometric mean of the } F_1 = \sqrt{\overline{P}_1 . \overline{P}_2}$$

$$\text{Geometric mean of the } F_2 = \sqrt{\tfrac{1}{2}\,(\overline{P}_1 + \overline{P}_2).\ \overline{F}_1}$$

The degree of dominance was revealed by comparing the expected arithmetic mean with the observed mean of the F_1, F_2 generations. The agreement between the observed and the arithmetic means of a given population indicates absence of dominance. A partial dominance is indicated when the observed mean of a given population stands between its arithmetic mean and the observed mean of one of the parents. Complete dominance is expected when the observed mean of the F_1 is not significantly different from the mean of a certain parent. Overdominance exists when the observed F_1 mean exceeds that of the higher parent or lower than the lower parent.

The nature of gene action was determined by comparing the expected arithmetic and geometric means of F_1 and F_2 with the observed mean of each population. Arithmetic gene action indicates that the effects of individual genes upon the genotype are additive, while geometric gene action assumes multiplicative action.

Wingan (12) and Mather (7) reported that the ratio of $\overline{F}_1 - M.P./\frac{1}{2}(\overline{P}_2 - \overline{P}_1)$, in a case of polygenic allelomorphs, is a measure of relative potency of gene sets. M.P. denotes the average of the two parents, P_2 is the parent with the high value and $\overline{P}_1$ is the parent with the low value. A value of 1.0 indicates complete dominance, and a value of 0.0 suggests no dominance.

Skewness of F_2 population was calculated according to the following formula:

$$SK = \frac{3\ (\text{Mean}-\text{Median})}{\text{standard deviation}}$$

A positive skewness indicates an excess in the number of items smaller than the mean, whereas the negative skewness indicates an excess of items larger than the mean.

The number of effective genes controlling each character was calculated using two formulas. The first was the Castle and Wright formula:

$$N = \frac{D^2}{8({}^{V}F_2 - {}^{V}F_1)}$$

where N is the minimum number of gene pairs by which the parents differ.

${}^{V}F_2$ is the F_2 variance.

${}^{V}F_1$ is the F_1 variance.

D is the difference between the two parental means.

The other formula was suggested by Wright:

$$N = \frac{0.25\ (0.75 - h + h^2)\ D^2}{{}^{V}F_2 - {}^{V}F_1}$$

where $h = \dfrac{\overline{F}_1 - \overline{P}_1}{\overline{P}_2 - \overline{P}_1}$

$D = \overline{P}_2 - \overline{P}_1$

$\overline{P}_1$ = the mean of the smaller parent.

$\overline{P}_2$ = the mean of the larger parent.

Heritability values measure the relative magnitude of genetic and non-genetic variance. Heritability (H) in broad sense would be:

$$H = \frac{{}^{V}F_2 - {}^{V}E}{{}^{V}F_2} \times 100$$

where V_E is the environmental variance and represent the average of the three variances of P_1, P_2 and F_1.

${}^{V}F_2$ is the variance of F_2 population.

The expected genetic advance from selection (G_s) for a given trait was estimated according to the following formula:

$$G_s = K.P^{\sigma}.H$$

where K is the selection differential in standard units
(K = 2.06 when selection intensity is 5%)
P^{σ} is the phenotypic standard deviation.
H is the heritability coefficient estimated as the ratio formed by dividing the genotypic by the phenotypic variance.

Most of the above mentioned formulas were used by Weber and Moorthy (11), Falconer (3), Allard (2) and Nishi and Kuriyama (9).

RESULTS

1. Earliness

The frequency distribution, mean number of days elapsed from transplanting to maturity, variance, and coefficient of variation of the parents, F_1, and F_2 generations of the two crosses are presented in Table 1. The frequency distributions are depicted in Figures 1 and 2.

In the first cross (Behairy–late × Giza 6M–moderate earliness), the P_1, P_2, F_1, and F_2 generations matured after 132–165, 117–144, 126–147, and 126–165 days with the means of 147.61 ± 0.63, 130.99 ± 0.46, 138.06 ± 0.60, and 145.15 ± 0.52 days and coefficient of variation of 5.76%, 5.46%, 4.32% and 6.36% for the four populations respectively. The model class in the F_2 was 147 days and included 195 out of 1,147 plants. There were 378 plants above the model class and 574 plants below it.

In the second cross (L 1421–late × L 324–early), the P_1, P_2, F_1 and F_2 generations matured after 129–150, 111–126, 126–147 and 117–150 days with the means of 140.39 ± 0.45, 118.31 ± 0.36, 137.84 ± 0.49 and 134.45 ± 0.32 days and coefficient of variation of 3.33%, 2.86%, 4.08% and 5.04% for the four populations respectively. The model class in the F_2 was 135 days and included 107 out of 450 plants. There were 166 plants above the model class and 177 plants below it.

Nature of dominance: As presented in Table 2, the observed F_1 mean of the first cross was lower than its arithmetic mean indicating a partial dominance of earliness. This conclusion was confirmed by potency value of −0.302. The observed F_2 mean was higher than its arithmetic mean indicating partial dominance of lateness over earliness. The 't' test of significance showed significant differences between F_2 observed mean and Behairy mean confirming partial dominance of Behairy parent. In the second cross the F_1 observed mean was higher than its arithmetic mean indicating partial dominance of lateness over earliness. The 't' test of significance showed significant difference between F_1 mean and L 1421 mean showing partial dominance of L 1421 parent. Potency of 0.587 confirmed such conclusion. The F_2 observed mean was higher than its arithmetic mean indicating partial dominance of lateness over earliness. The F_2 distributions of both crosses showed negative skewness and indicated an excess of items greater than the mean, i.e. toward lateness. Skewness was significant in the second cross.

Nature of gene action: Comparisons of the arithmetic and the geometric means versus the observed ones for F_1 and F_2 of both crosses did not give a clear trend concern-

Table 1 Frequency distributions for earliness of maturity of the P_1, P_2, F_1 and F_2, generations in Behairy × Giza 6 M and L 1421 × L 324 crosses.

Cross		No. of days																			Total	Mean and	Vari-	C.V.
No.	Generation	111	114	117	180	123	126	129	132	135	138	141	144	147	150	153	156	159	162	165	n	$S_{\bar{X}}$	ance	%
	P_1 (Behairy)[a]								5	8	14	22	38	16	19	18	11	13	7	7	178	147.61 ± 0.63	72.23	5.76
1.	P_2 (Giza 6 m)[b]			7	9	12	37	52	50	29	21	11	12								240	130.99 ± 0.46	51.14	5.46
	F_1						3	3	12	10	28	23	8	6							93	138.06 ± 0.60	35.64	4.32
	F_2						9	25	31	76	112	151	170	195	167	104	50	42	12	3	1147	145.15 ± 0.52	85.23	6.36
	P_1 (L 1421)[a]							2	8	13	19	28	25	12	2						109	140.39 ± 0.45	21.80	3.33
	P_2 (L 324)[c]	4	12	32	26	12	3														89	118.31 ± 0.36	11.45	2.86
2.	F_1						5	13	14	13	30	27	18	10							130	137.84 ± 0.49	31.72	4.08
	F_2			4	10	26	35	43	59	107	67	47	33	9	10						450	134.45 ± 0.32	45.84	5.04

[a] = late
[b] = moderate earliness
[c] = early.

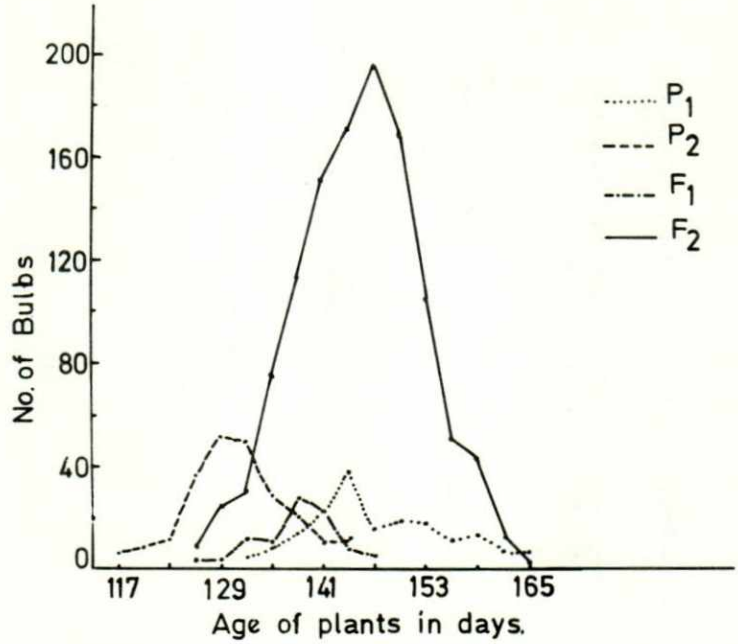

Fig. 1. Frequency distributions of earliness of maturity in the cross between Behairy × Giza 6 M.

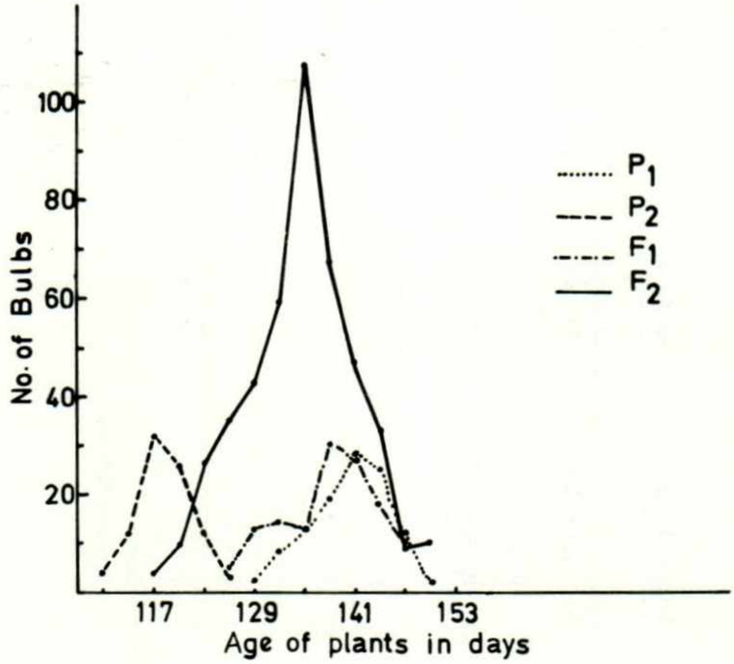

Fig. 2. Frequency distributions of earliness of maturity in the cross between L 1421 × L 324.

Table 2 Means of parents, observed means of F_1 and F_2, expected arithmetic and geometric means of F_1 and F_2, potency, skewness, minimum number of genes, heritability and expected genetic advance for earliness in Behairy × Giza 6 M and L 1421 × L 324 crosses.

	Behairy × Giza 6 M				L 1421 × L 324			
	Generation				Generation			
Cross	P_1	P_2	F_1	F_2	P_1	P_2	F_1	F_2
	Behairy (late)	Giza 6 M Med. (early)			L 1421 (late)	L 324 (early)		
Means:								
Observed	147.61 ± 0.63	130.99 ± 0.46	138.06 ± 0.06	145.15 ± 0.52	140.39 ± 0.45	118.31 ± 0.36	137.84 ± 0.49	134.45 ± 0.32
Arithmetic			139.30	138.68			129.35	133.59
Geometric			139.05	138.66			128.88	133.53
Mean differences:								
Observed vs observed	16.62[b]				22.08[b]			
Observed vs arithmetic			1.24[a]	6.47[b]			8.49[b]	0.86
Observed vs geometric			0.99 n.s.	6.49[b]			8.96	0.92[a]
Potency			−0.302				+0.587	
Skewness				−0.111 n.s.				−0.174
No. of genes:								
Castle and Wright				0.69				4.36
Wright				0.75				5.59
Heritability %				37.80				52.75
Expected genetic advance (P = 0.05)				7.19				7.36
Expected genetic advance in percent of F_2 means				4.95				5.47

[a] Significant (0.05 level)
[b] Highly significant (0.01 level)

ing the nature of gene action. However, the F_1 results of the first cross showed the presence of multiplicative gene action.

Number of genes involved: The Castle and Wright's and Wright's formulae gave estimates of 0.69 and 0.75 pair of genes respectively, Table 2. These estimates suggested that the difference between the two parents Behairy and Giza 6 M with regard to earliness character might be governed by one pair of genes. The other possibility is that the assumptions on which these formulae are based, are not fulfilled and subsequently gave a value smaller than the true one. However, some of the extreme parental classes of Giza 6 M were not completely recovered in F_2 suggesting the presence of more than one gene. In the second cross, the two estimates were 4.36 and 5.39 pairs of genes, respectively, Table (2). These estimates suggested the presence of 4–6 pairs of genes controlling the difference in earliness in this cross. Also, some extreme classes of the early parent L 324 were not recovered in F_2.

Heritability and gentic advance: The heritability estimate in the first cross, Table 2, was low and indicated that selection for earliness would not be very effective. Based on heritability estimate of this cross, and by selecting the earliest 5% of the F_2 plants, the expected gain in F_3 could be 7.19 days. The F_3 mean would be expected to be shifted 4.95% earlier than the F_2 mean in this cross. The heritability value in the second cross was 52.75% and indicated that selection for earliness can be moderately effective. The selection of 5% of F_2 plants would result in an expected genetic advance of 7.36 days in F_3 of this cross.

2. Bulb weight:

The frequency distributions, means, variances and coefficients of variation of the parents, F_1 and F_2 generations of the two crosses are presented in Table 3. The frequency distributions are depicted in Figures 3 and 4.

In the first cross, the bulb weight in P_1, P_2, F_1 and F_2 generations ranged from 70–230, 30–130, 10–110 and 10–250 grams with the means of 138.82 ± 2.88, 85.26 ± 2.06, 76.21 ± 2.03 and 100.24 ± 2.24 grams and coefficient of variation of 20.80%, 24.34%, 24.79%, and 49.99% for the four populations, respectively. The model class in F_2 was 50 grams and contained 81 out of 500 plants. There were 332 bulbs above the model class and 87 bulbs below it.

In the second cross (L 1421 × L 324), bulb weight in P_1, P_2, F_1 and F_2 generations ranged from 10–150, 10–150, 10–110, 10–230 grams with the means of 76.32 ± 3.12, 95.57 ± 2.82, 83.13 ± 2.31 and 78.05 ± 1.97 grams and coefficient of variation of 40.93%, 29.55%, 38.84% and 50.24% for the four populations respectively. The model class in F_2 was 50 grams and contained 93 out of 400 bulbs. There were 198 bulbs above the model class and 109 bulbs below it.

Nature of dominance: As presented in Table 4, there was a highly significant difference between the observed versus the arithmetic means of F_1 generation of the first cross. That was evidence of the presence of a certain degree of dominance. The observed F_1 mean was significantly lower than Giza 6 M mean indicating the occurrence of heterosis. The high and negative value of potency (−1.33) was further evidence of overdominance. The F_2 observed mean was higher than its arithmetic. It was closer to the mean of the Giza 6 M parent as indicated by F_2 skewness. This ascertained the overdominance of the small bulb weight. In the second cross, the F_1 observed mean was significantly lower than its arithmetic mean. It was significantly smaller than the L 1421 parent that was characterized by small bulb weight. Potency value was −2.88. This

Table 3 Frequency distributions for the bulb weight of the P_1, P_2, F_1 and F_2 generations in Behairy × Giza 6 M and L 1421 × L 324 crosses.

Cross No.	Generation	Bulb weight in grams													Total	Mean and $S_{\bar{X}}$	Variance	C.V.%
		10	30	50	70	90	110	130	150	170	190	210	230	250				
	P_1 (Behairy)				1	13	32	30	13	4	4	1	2		100	138.82 ± 2.88	833.89	20.80
1.	P_2 (Giza 6 M)		1	27	31	28	12	1							100	85.26 ± 2.06	423.43	24.34
	F_1	2	11	25	39	22	2								101	76.21 ± 2.03	418.02	24.79
	F_2	15	72	81	72	71	57	51	39	13	13	9	5	2	500	100.24 ± 2.24	2511.75	49.99
	P_1 (L 1421)	1	16	36	21	12	8	5	1						100	76.32 ± 3.12	975.98	40.93
2.	P_2 (L 324)	1	5	9	19	44	11	8	3						100	95.57 ± 2.82	797.38	29.55
	F_1	17	19	24	39	12	2								113	63.13 ± 2.31	601.06	38.84
	F_2	35	74	93	61	55	46	18	9	5	2	1	1		400	78.05 ± 1.97	1537.68	50.24

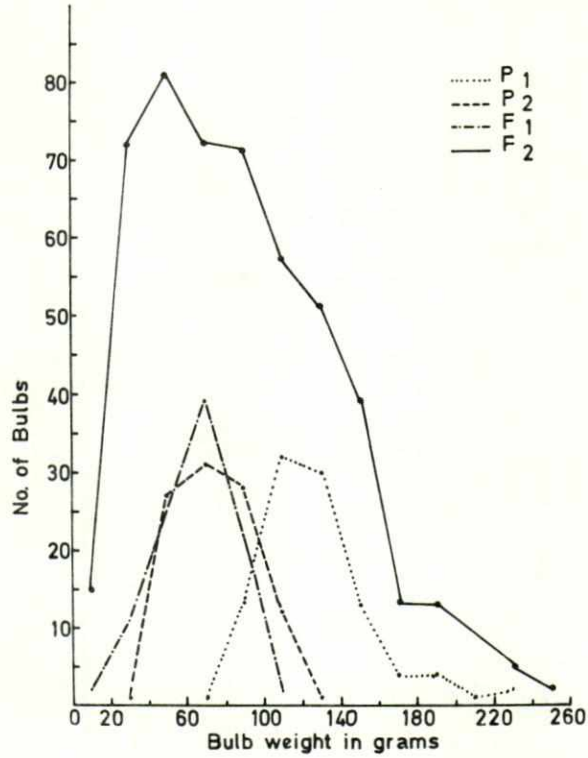

Fig. 3. Frequency distributions of bulb weight in the cross Behairy × Giza 6 M

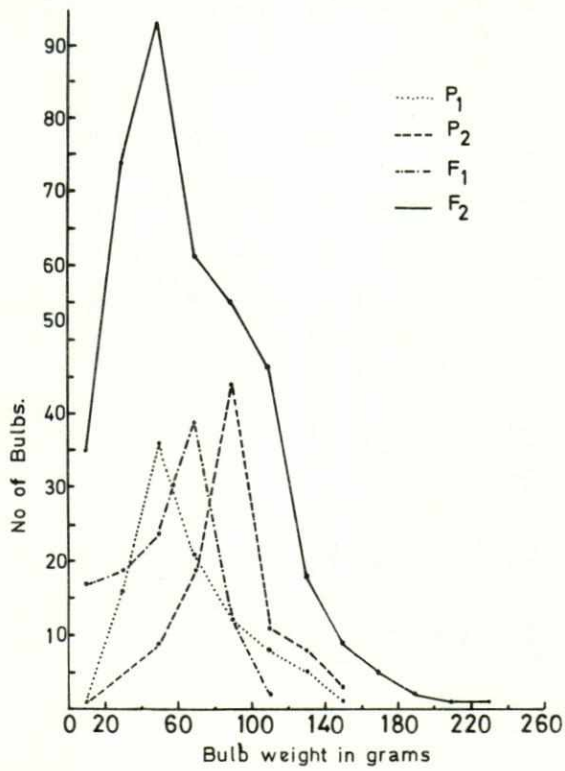

Fig. 4. Frequency distributions of bulb weight in the cross L 1421 × L 324.

Table 4 Means of parents, observed means of F_1 and F_2, expected arithmetic and geometric means of F_1 and F_2, potency, skewness, minimum number of genes, heritability and expected genetic advance for bulb weight in Behairy × Giza 6 M and L 1421 × L 324 crosses.

	Behairy × Giza 6 M				L 1421 × L 324			
	Generation				Generation			
Cross	P_1	P_2	F_1	F_2	P_1	P_2	F_1	F_2
	Behairy	Giza 6 M			L 1421	L 324		
Means:								
Observed	138.82 ± 2.88	85.26 ± 2.06	76.21 ± 2.03	100.24 ± 2.24	76.32 ± 3.12	95.57 ± 2.82	63.13 ± 2.31	78.05 ± 1.97
Arithmetic			112.04	94.13			85.95	74.54
Geometric			108.80	92.36			85.40	73.66
Mean differences:								
Observed vs observed	53.56[b]				19.25[b]			
Observed vs arithmetic			35.83[b]	6.11[a]			22.82[b]	3.51 n.s.
Observed vs geometric			32.59[b]	7.88[b]			22.27[b]	4.39[a]
Potency			−1.33				−2.38	
Skewness				+2.170[b]				+1.416[b]
No. of genes:								
Castle & Wright				0.17				0.49
Wright				0.43				0.53
Heritability %				77.77				48.53
Expected genetic advance (P = 0.05)				80.54				39.17
Expected genetic advance in percent of F_2 means				80.35				50.19

[a] Significant (0.05 level)
[b] Highly significant (0.01 level)

indicated the overdominance of small bulb weight. The F_2 observed mean was not significantly different from its arithmetic mean but was insignificantly different from the mean of the small parent L 1421. This verified the overdominance of small bulb weight. The F_2 distributions of both crosses, showed positive and highly significant skewness and indicated an excess of items smaller than the mean, i.e. towards small bulb weight.

Nature of gene action: In the first cross, it was impossible to determine the nature of gene action because the observed means of F_1 and F_2 deviated significantly from the respective arithmetic and geometric ones. In the second cross, the F_1 observed mean was significantly lower than its arithmetic and geometric means. The F_2 observed mean was not significantly different when compared with its arithmetic mean, but was significantly higher than its geometric mean. The F_2 results indicated that the gene action was additive in nature.

Number of genes involved: Castle and Wright's and Wright's formulae gave a low estimate of the minimum number of genes involved in the inheritance of bulb weight in both first and second crosses. The F_2 distributions of both crosses covered both parental ranges suggesting the presence of a small number of genes governing bulb weight.

Heritability and genetic advance: Heritability values were shown in Table 4. A high heritability of 77.77% in the first cross indicates that selection for bulb weight could be highly effective in the F_2 of this cross, while the value 48.53% of the second cross indicates a moderate effectivness of selection. Planting the top 5% of the F_2 plants in F_3 would result in an increase of the F_3 mean by about 80.54 and 39.17 grams in the first and second cross respectively.

DISCUSSION

1. Earliness

The number of days from transplanting to maturity time at which the top of the bulb falls down, was taken as an indication of earliness. Populations of Behairy and Giza 6 M cultivars, as indicated in Table 2, differ significantly from each other, with the second significantly earlier than the first. In addition, the line L 324 was significantly earlier than L 1421. It is known that Behairy is adapted to lower Egypt and Giza 6 M to upper Egypt conditions. The geographic diversity of the two cultivars may have given rise to different genetic constitutions controlling maturity.

The F_2 of the first cross and F_1, F_2 distributions of the second cross suggested partial dominance of lateness. The only exception to this is the F_1 of the first cross that showed partial dominance of earliness. This deviation may be attributed to the relatively small difference with regard to earliness between Behairy and Giza 6 M parents as compared with the difference between L 1241 and L 324 parents of the second cross. F_2 distributions of both crosses showed skewness toward lateness, but it was significant skewness in the second cross only.

Comparisons of the arithmetic and geometric means versus the observed ones of F_1 and F_2 in both crosses did not permit the determination of the nature of gene action, with the exception of F_1 results of the first cross that indicated the presence of multiplicative gene action.

In both crosses, some of the extreme parental classes of Giza 6 M and L 324 were not completely covered in F_2 suggesting the presence of more than one pair of genes governing the inheritance of maturity time in onions. Estimates of the number of genes involved in the second cross suggested the presence of four to six pairs of genes.

Relatively low 37.8% and moderate 52.75% heritability estimates were obtained in this study in the first and second cross, respectively. These values would permit relatively moderate effective selection of individual plants for earliness in the F_2 population. The expected genetic gain in F_3 could be 7.19 and 7.36 days in the first and second cross, respectively. Based on 5% selection intensity, the F_3 mean would be expected to be shifted 4.95–5.47% earlier than the F_2 means in the first and second cross, respectively.

Some reports in literature on the inheritance of earliness are available. Orlova (10) made various crosses and indicated that earliness showed intermediate inheritance. Further, Hosfield *et al.* (4), reported that maternal influences were important for maturity.

2. Bulb weight

Small bulb weight of Giza 6 M was overdominant to large bulb weight of Behairy cultivar. This conclusion was confirmed in the second cross involving the small bulb weight parent L 1421 and the large bulb weight parent L 324. The second cross indicated that the gene action is additive in nature, while the determination of gene action was difficult in the first cross.

The results obtained from both crosses suggested that at least one pair of genes control the difference in bulb weight. The F_2 distributions of both crosses covered both parental ranges indicating the presence of a small number of genes controlling bulb weight.

High to moderate heritability values were obtained, 77.77% for the first cross and 48.53% for the second cross. This would make the individual plant selection highly or moderately effective and would increase the genetic gain in the following generations. Some reports in the literature disagreed with the heritability values estimated in the present investigation. McCollum (8) reported that heritability values were in general low or zero for bulb weight. This disagreement may be attributed to the utilization of different plant material.

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