GENETIC STUDIES ON EGGPLANT (*SOLANUM MELONGENA* L.)

III. FURTHER INVESTIGATIONS REGARDING THE DEGREE OF HERITABILITY AND THE NUMBER OF EFFECTIVE FACTORS*

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An adequate estimation of heritability of the quantitative and aggregate characters plays a significant and important role in selection. Various methods of estimating heritability, based on the same principle, have been devised by many workers in recent years. A few results with regard to the heritability of seven quantitative characters in five eggplant crosses were reported by the author (3). They showed that the degree of heritability in broad sense was different for various characters and in various crosses. The heritability of the yield and the number of fruits per plant was very low, while that of the period from seeding to flowering, fruit shape, fruit weight, bunchiness, and hairiness was generally high. But the F_1 variances do not always represent the true environmental variances in the segregating generations. Therefore, in the present study the heritability of three characters was estimated using the parent-offspring regressions in the F_2 - and F_3 -generations. Estimates thus obtained should be more correct than on the basis of F_1 variances. Under the same design, it was also attempted to resolve the variation of the same characters in the segregating populations into its components, namely D, H, E_1 and E_2 , and to estimate the number of effective factors governing the given traits by the procedure proposed by Mather (4).

Materials and Methods

Two most interesting crosses were chosen from five crosses examined last year, namely, a) Florida high bush $\times$ Sendai-naga No. 1 and b) Turuboso-sen-nari $\times$ Taiwan-naga. About 10 per cent of the F_2 plants of both crosses were selfed at random and their progenies were used in this study. The F_3 generations consisted of 21 families of the former and 9 families of the latter cross. Though the number of F_3 families in the latter cross may be, theoretically, too small for statistical computations, the results are worth mentioning.

The dates of seeding and transplantation to the field were May 28th, and June 26th for the former cross and May 18th and June 19th for the latter cross, respectively. Seedlings were planted 50 cm apart in rows spaced 1 m apart in a randomized block arrangement with four replications. Records for the length of the period from seeding to first flower, fruit shape, and fruit weight were taken for each plant of the parent varieties, the F_2 - and the F_3 -populations. 12, 48, and 6 plants per plot for the parents, the F_2 - and the F_3 -generations were examined in a block.

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The date of the opening of the first flower on each plant was recorded every other day. When the fruits attained nearly full growth, two per plant were taken, and their shape and weight were determined. The fruit shape was expressed by the shape index, i.e. the ratio of length to width. Data for the weight per fruit were transformed into logarithms, according to the procedure described in the preceding paper [Gotoh (2)].

The degree of heritability was estimated by the parent-offspring regressions. Regressions were computed by dividing the covariance of the previous year's F_2 plants and their progeny by the variance of F_2 plants, i.e. $\frac{W_{F_2/F_3}}{V_{F_2}}$.

Heritability in broad sense was also estimated. Averaged variance of both parents was used as the environmental variance, and the degree of heritability was estimated by dividing the variance of F_2 plants minus environmental variance by the variance of the former, i.e.

$$\frac{V_{F_2} - \frac{1}{2}(V_{P_1} + V_{P_2})}{V_{F_2}}.$$

The procedure of estimating the number of effective factors was in accord with the scheme presented by Mather(4). Then the so-called K_1 and K_2 were computed by the formulae

$$K_1 = \frac{\frac{1}{2}(\bar{P}_1 - \bar{P}_2)^2}{D} \text{ and } K_2 = \frac{\left(\frac{1}{4}D + \frac{1}{8}H\right)^2}{V_{VF_3}}.$$

$\bar{P}_1$ and $\bar{P}_2$ being the mean values for the parents, D and H the fixable and unfixable components of variation in the genetic portion of segregating populations, and V_{VF_3} the variances of variances of all the families in F_3 . However, a correction term $\left(\frac{2}{n-1}V_{F_3}^2\right)$ was deducted from V_{VF_3} , according to Fisher's proposal.

Throughout the summer of 1953, the climatic conditions were unfavorable. Thus, the flowering time was more or less delayed, and some other difficulties were encountered, as indicated later.

Experimental Results

a) Statistics of populations

Table 1 shows the means for the parents, and the F_2 - and F_3 -populations for the three characters measured in 1953, and the corresponding means for the parents, F_1 and F_2 in 1952. In this table, as well as in the later tables and text, *Fl*, *Se*, *Tu*, and *Ta* stand for the names of the parental varieties, namely, Florida high bush, Sendai-naga No. 1, Turuboso-senari, and Taiwan-naga, respectively. As shown in this table, the difference between the parents regarding each character is striking especially between *Fl* and *Se*. Except for the period from seeding to flowering in the *Fl* × *Se* cross, the differences between the means in 1952 and those in 1953 were small. Though the seeding dates in 1953 were the same or 10 days earlier than in 1952 for the crosses *Fl* × *Se* and *Tu* × *Ta*, the flowering time of the parents and F_2 populations were delayed in 1953. Further, the fruits of the parents and F_2 were

Table 1. Means of parents, F_1 , F_2 and F_3 populations in 1952 and 1953.

Crosses	Genera- tions	1953			Genera- tions	1952		
		Period from seeding to flowering (days)	Shape index	Fruit weight (log)		Period from seeding to flowering (days)	Shape index	Fruit weight (log)
$Fl \times Se$	P_1	127.5	1.64	2.65	P_1	108.0	1.76	2.66
	P_2	99.9	6.75	1.90	P_2	89.0	7.36	1.86
	F_2	111.1	3.65	2.13	F_1	95.9	3.99	2.19
	F_3	112.8	3.22	2.06	F_2	99.0	4.03	2.17
$Tu \times Ta$	P_1	98.2	1.77	1.88	P_1	87.3	1.85	1.97
	P_2	109.8	5.34	2.22	P_2	102.0	6.04	2.24
	F_2	113.2	3.40	2.02	F_1	98.5	3.85	2.21
	F_3	104.0	3.31	1.98	F_2	99.8	3.74	2.14

shorter and their weight was lighter in 1953 than in 1952. This was mainly due to the unfavorable conditions during the summer of 1953. The F_3 means for shape index and fruit weight show lower values than the corresponding F_2 means. To some extent, dominance effects of the genes governing these characters are likely concerned with those relations. However, the F_3 families may be too small to allow a conclusive opinion.

The second-degree statistics for parents, F_2 and F_3 , i.e. the variance of both parents and F_2 , the variance of the F_3 families, the mean variance of the F_3 families, and covariance between the F_2 individuals and the F_3 families were computed. Within these statistics, the differences between the crosses with respect to the F_2 variance were particularly interesting. Table 2 gives the F_2 variances for the three characters in each cross in 1952 and 1953. In spite of the wide difference between the parents, the F_2 variance of the period from seeding

Table 2. Variances of F_2 populations in 1952 and 1953.

Characters	Crosses	1953	1952
Period from seeding to flowering	$Fl \times Se$	53.01	18.34
	$Tu \times Ta$	194.16	50.25
Shape index	$Fl \times Se$	1.1536	1.5768
	$Tu \times Ta$	0.5966	0.5922
Fruit weight	$Fl \times Se$	0.0208	0.0108
	$Tu \times Ta$	0.0182	0.0199

to flowering in the $Fl \times Se$ cross was the smallest among the five crosses in 1952. In the same manner, the F_2 variance of this trait in the $Fl \times Se$ cross was nearly one third of the F_2 variance in the $Tu \times Ta$ cross in 1952 and one fourth of that in 1953. The opposite was true for the shape index of two crosses. Thus, it appears entirely probable that the effects of genes governing each trait are different in the two cases. The first question is, to which sort of genes is the F_2 variation attributable, polygenes or major genes? Of course, some other factors affecting the F_2 variance may be surmised, such as a difference in vigor of the

F₂ populations, action of linkages and effect of dominance. In some instances they may play a significant role. However, all these suppositions are at present untenable. In the *Fl* × *Se* cross, the variation of the period from seeding to flowering in F₂ may be controlled by polygenes, and the variation of fruit shape may be affected by major genes. In the *Tu* × *Ta* cross, the variation of the former trait is governed strongly rather by major genes than polygenes, and that of the latter trait may be conditioned by polygenes. Distribution curves of each trait for the F₂ populations in 1952 and 1953 confirmed these assumptions. Moreover, the figures of the frequency distributions in each year were similar, except the slight transition of the modes. A bimodal frequency distribution was observed in the F₂ variation for the period from seeding to flowering in the *Tu* × *Ta* cross and for the fruit shape in the *Fl* × *Se* cross. The other curves showed a unimodal or nearly normal distribution, indicating a so-called polygenic variation. The F₂ variance of fruit weight in each cross was about the same in both years, and their variations showed a unimodal distribution. Hence, it may be expected that the genes governing fruit weight have polygenic effects. The relationships between the magnitude of the F₂ variance and the degree of heritability will be discussed later. The results of the variance analysis based on the means for each trait in each plot showed that all of the differences between the replications were non-significant. Consequently, the means and the variances of each population were computed without any correction between the blocks.

b) Heritability

The degree of heritability of the three characters estimated by the parent-offspring regressions is presented in Table 3, and the corresponding heritability in broad sense is also given. Heritability estimated by the former method will give more adequate values, when

Table 3. Heritability in per cent for the three characters in each cross.

Characters	by the parent-offspring regressions		in broad sense	
	<i>Fl</i> × <i>Se</i>	<i>Tu</i> × <i>Ta</i>	<i>Fl</i> × <i>Se</i>	<i>Tu</i> × <i>Ta</i>
Period from seeding to flowering	64.8	75.7	3.0	77.6
Shape index	74.9	66.4	60.9	60.1
Fruit weight	60.0	47.6	57.9	38.8

the dominance effects are negligible, i.e. when there is no dominance or nearly so. But it may be expected that such a method is, at least, more efficient than estimating the environmental variances by the variances of the parents or F₁ population.

The degree of heritability of the period from seeding to flowering, shape index, and fruit weight were 65 to 78, 60 to 75 and 40 to 60 per cent respectively. Except for the period from seeding to flowering, the degrees of heritability of each trait are relatively low, in comparison with the degree of heritability as obtained by using the environmental variances as represented by the F₁ variances of the previous year. Thus, it is presumable that the F₁

variances may not represent the true non-heritable portion of variance in segregating populations. This will be discussed in the later part of this paper.

The degree of heritability in broad sense for the period from seeding to flowering in the $F_1 \times Se$ cross was unexpectedly low. This result may be interpreted according to the finding regarding the F_2 variance, as mentioned above in connection with Table 2. Further, we must take into account the possibility that the parental populations have a lower vigor than the hybrid populations and are more sensitive to environmental variations than the segregating populations having normal vigor. In fact, the averaged variance of the parents for the given trait was even slightly smaller than the F_2 variance.

c) Number of effective factors

Parents, F_2 and F_3 were used in estimating the number of the effective factors governing the period from seeding to flowering, shape index, and fruit weight. Two interesting questions arose, in what way are the factors expressing such traits distributed in both parents? And, whether the effects of individual factors are similar or not? Table 4 shows the components of variation obtained by least squares calculation.

Table 4. The components of variation partitioned by the least squares calculation.

	$Fl \times Se$			$Tu \times Ta$		
	Period from seeding to flowering	Shape index	Fruit weight	Period from seeding to flowering	Shape index	Fruit weight
<i>D</i>	120.9011	2.3788	0.026301	-4.4230	0.9864	0.010624
<i>H</i>	-257.5327	-1.7249	0.005281	528.4379	-0.3040	-0.008677
<i>E</i> ₁	60.8731	0.3186	0.014545	45.5512	0.1703	0.011766
<i>E</i> ₂	7.7926	-0.0376	0.002923	21.7405	0.0418	0.000055

Table 5. Number of effective factors.

Characters	$Fl \times Se$		$Tu \times Ta$	
	K_1	K_2	K_1	K_2
Period from seeding to flowering	1.58	0.63	—*	1.98
Shape index	1.77	2.20	3.23	1.07
Fruit weight	5.35	0.48	2.72	1.02

* Not included on account of negative value.

According to these statistics, the number of the effective factors, the so-called K_1 and K_2 , was computed. The results obtained are presented in Table 5. In spite of the great difference between the parents, the number of the effective factors estimated was extremely low. Similar cases are frequently described in Mather's book (4), and such a case is, also, reported by Copp and Wright (1) in a wheat cross. Of course, the values estimated do not mean,

biometrically, the number of genes in general sense. But, since all the traits dealt with in our experiment are controlled by complicated interaction of many genic systems, it is difficult to gain reliable results, unless a more efficient method could be devised. Table 5 shows that the K_1 are generally larger than the K_2 . This will be discussed later.

d) Variation of the F_3 generation in the $Fl \times Se$ cross

The variety *Fl* has the largest, relatively round fruits and the latest flowering time, while almost the opposite is true for each trait of the variety *Se*. The F_3 hybrid population of this cross showed a striking segregation, and various segregants and recombinants were observed. It can be safely said that the segregation for the period from seeding to flowering occupies almost the whole range of variation of the cultivated varieties in Japan. The fruit shape of the segregants varied from slender and intermediate to round. The fruit weight of the segregants was varying from light to heavy. Lastly, similar phenomena were also observed in the habit of plants (erect or prostrate) and the leaf size. Table 6 shows an

Table 6. Extreme segregants in the F_3 population of the cross $Fl \times Se$.

Characters	Types	Number of F_3 family	Values of F_2 plant	Means of F_3 family	Values of the extreme segregants
Period from seeding to flowering (days)	early type	2	86	98	89
	"	4	93	100	87
	"	6	91	103	89
	late type	3	115	107	121
	"	5	103	131	140
	"	17	101	110	127
Shape index	round type	6	1.62	1.55	1.29
	"	9	2.09	1.92	1.45
	"	17	2.28	2.40	1.63
	slender type	7	4.82	5.44	6.52
	"	8	6.49	4.91	6.16
	"	12	4.76	3.96	5.02
Fruit weight (log)	light type	2	2.10	1.78	1.45
	"	4	2.03	1.83	1.36
	"	7	2.20	1.97	1.79
	heavy type	9	2.16	2.15	2.42
	"	12	2.23	2.15	2.35
	"	13	2.20	2.24	2.49

example of such a striking segregation. It can be seen that the parent types regarding each trait were recovered in the population, except for a few instances.

Discussion

The degree of heritability computed by the parent-offspring regressions gave reasonable values for each trait, and it was found that the heritability in broad sense for the shape

index and fruit weight was relatively high. In the previous experiment [Gotoh(3)] the variances of F_1 were used in the estimation of the environmental variance. It may be safely concluded that the variances of F_1 do not represent the true non-heritable portion of variances in the segregating generations, as questioned in the preceding paper, [Gotoh(3)]. But it cannot be overlooked that the reactions of the F_1 populations regarding the environmental variations are different with respect to the following properties. Fruit shape and fruit weight in F_1 were, generally, apt to give an extremely uniform impression. Hence, their variances in F_1 sometimes showed unexpectedly low values. On the contrary, the variances of the fruit yield or fruit number per plant in F_1 are affected by, or correlated with, high means attributable to heterosis. The variances for such traits, eventually, tend to give over-high values as compared with the non-heritable variation in the segregating generations. Besides, the eggplant varieties in general are relatively sensitive to the environment. All these phenomena exert a greater or lesser influence on the estimates of heritability in broad sense, as also suggested by Warner (5).

WF_2/F_3 , the covariance of the F_2 plants of the previous year and their progenies, includes the unfixable genetic variation. Thus, the heritability estimated by the formula $\frac{WF_2/F_3}{VF_2}$ may indicate the net value in narrow sense so far as the dominance effects are negligible. In our experiments, the F_2 plants and their progenies were grown in two different years, but it is yet uncertain, in what manner the interaction between genotype and year factor affects the regression estimates. These weakness must be taken into account in estimating heritability by the parent-offspring regressions.

The magnitude of the F_2 variances for the three traits was compared for the two crosses, as shown in Table 2. It is assumed that in $Fl \times Se$ the difference in the period from seeding to flowering, in $Tu \times Ta$ the difference in shape index and in both these crosses the fruit weight are governed by polygenic systems. On the other hand, in $Tu \times Ta$ the difference in the period from seeding to flowering, and in $Fl \times Se$ the difference in the shape index are attributed rather to major genes than to polygenes. These assumptions were verified by means of comparison of the frequency distributions. Further, the number of factors concerned and the magnitude of the effects of individual factors may affect the degree of heritability of a given trait. As shown in Table 3, the degree of heritability for the period from seeding to flowering in $Fl \times Se$ is higher than that in $Tu \times Ta$, and, on the contrary, that for the shape index of the former cross is lower than that in the latter cross. These relations were found also in the preceding paper. Hence, the above mentioned assumptions are confirmed not only by means of comparison of the frequency distribution in F_2 , but also by means of comparison of the degree of heritability.

The performance in the estimation of the number of the effective factors was in general unsuccessful. But Table 5 shows that the values of K_1 are greater than those of the corresponding K_2 in four cases of five. This relation suggests that the plus or minus factors governing the given traits are almost completely concentrated in one parent. Furthermore, the value of K_2 estimated for the fruit weight in $Fl \times Se$ was extremely small, comparing

with that of the corresponding K_1 . Thus, it is expected that the effects of the factors underlying this trait may not be similar, under the assumption that this trait is controlled by polygenic systems.

In Table 6, the extreme segregants for each trait in F_3 of the cross $Fl \times Se$ are given. A remarkable segregation was observed between these extremes, and various recombinants of many traits were also found. It is very interesting that a great deal of the segregants and recombinants, which occupy almost the whole range of variation of the cultivated varieties, were represented in the F_3 population. Such phenomenon poses some problems. One of them deals with the origin and evolution of many eggplant varieties, which are widely adapted all Japan over. The observations that quantitative characters control the variations of most of the traits of eggplant varieties, and, conversely, major genic differentiations occur only in a few traits in Japan, are suggestive regarding this problem. According to Vavilov's opinion (6), the eggplant (*Solanum melongena* L.) has two ancestral forms. One belongs to the so-called Chinese Gene Center, and the other to the Indian Gene Center; a special form with small fruits is characteristic of the former. If these findings are reliable, the question arises, from which center are derived the varieties naturalized in Japan? and is it possible to distinguish varieties of the two centers by some definite characteristics? In connection with the above mentioned remarkable segregation in a hybrid population, it would be of interest to find out, to what mechanisms a great deal of the variation in the quantitative traits of eggplant varieties is attributable? Further, it is possible that the degree of heterosis in eggplant, which is generally observed in F_1 hybrids, is associated with the origin of the varieties. These problems are so complicated that it is difficult to deduce safe conclusions under present conditions. Such combinations of parents as in the cross $Fl \times Se$, is also interesting for practical breeding, and new valuable recombinants may be expected from such material.

Summary

1. Heritability of three quantitative characters was estimated in two eggplant crosses. The degrees of heritability for the period from seeding to flowering, fruit shape index, and fruit weight were 65-78, 60-75 and 40-60 per cent respectively.
2. Heritability for the fruit shape index and fruit weight estimated by parent-offspring regressions was relatively low, as compared with heritability for them in broad sense, when the variances of F_1 were used for the estimation of the environmental variances. In connection with this finding, it was concluded that the F_1 variances used as environmental variances of the segregating generations give too large or too small values, according to the traits.
3. The remarkable differences between the F_2 variances of both crosses were interpreted as due to effects of genes (polygenes or major gene) governing such traits. This assumption was verified by the frequency distribution in F_2 , and its appropriateness was emphasized on the basis of the relationships between the effects of genes and the degree of heritability.
4. The number of effective factors was estimated by the procedure proposed by Mather
- (4). The estimates were generally low and they were not so reliable, but it was found that

the factors having plus or minus effects are probably concentrated within one parent.

5. Various segregants or recombinants were observed in the F_3 of the cross $Fl \times Se$, and the range of that segregation was occupying almost the whole range of variation of the cultivated varieties. It may be expected in practical breeding to obtain many new variants from such cross combinations.

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