STUDIES ON THE QUALITATIVE AND QUANTITATIVE INHERITANCE OF AN INTERSPECIFIC CROSS OF SOYBEAN, *GLYCINE MAX*×*G. FORMOSANA*[1]

WEN-TONG TANG and GEORGE TAI[2]

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Introduction

Interspecific crossing experiments between the cultivated soybean, *Glycine max* Merrill, and other *Glycine* spp. have been carried out by several investigators (Fukuda, 1933; Karasawa, 1936; Ting, 1936; Williams, 1948; Weber, 1950), but only two species, *i.e. G. ussuriensis* and *G. gracilis,* have been successfully crossed with the cultivated variety. *G. ussuriensis,* which grows wild throughout the Eastern Asia, possesses some characters quite different from *G. max,* such as prostrate growth; long, fine, twining stem; small, narrow leaves; small, compressed pods; and small, oblong seeds of a sooty black color. *G. gracilis,* however, has characters intermediate between the wild and the cultivated species and is distributed as a wild one. Piper and Morse (1923) reported that in *G. gracilis* a number of strains were found which formed an almost continuous array of intergrades from the wild types to the domestic ones. Based on this ecological and morphological evidence, and accompanied by cytological study (all of three species have the same chromosome number, 2n=40), the general conclusion is that the change from the wild *G. ussuriensis* to the cultivated *G. max* is derived only from gene mutation, while the different forms of *G. gracilis* may be the intermediate products of evolution.

Many other tropical species of *Glycine* have been found, but their relations to the cultivated species still remain obscure. However, a subtropical wild-growing species named *G. formosana* Hosokawa (Hosokawa, 1930), which grows in Hsinchu Hsien, Taiwan, was hybridized to two cultivated varieties without any difficulties by Tang *et al* (1959). By a comparison of important characteristics between *G. ussuriensis* and *G. formosana,* the authors found that they were very much alike morphologically. Unfortunately, there was no standard strain

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(2) Professor and graduate student of College of Agriculture, National Taiwan University, Taipei, Taiwan respectively.

of *G. ussuriensis* at hand, so that information about *G. ussuriensis* was obtained indirectly from various papers and books. Direct studies about the relationship of these wild species and their respective affinities to *G. max* is still wanting.

This paper deals mainly with the genetic behavior of both qualitative and quantitative characters in the progeny of *G. max-formosana*. Although many characteristics are under study, only a few of them will be reported here.

Materials and Methods

One cultivated variety of *G. max*, Taichung Green, was chosen to be the female parent. This variety had a lot of characters different from those of the wild male parent, *G. formosana*. Crosses were made in 1957. F_1 seeds were grown in the green house for F_2 generation in 1958. And seeds from 20 unselected F_2 plants were separately collected for 20 F_3 lines in 1959.

In 1960, plants of all generations P_1 (Taichung Green), P_2 (*G. formosana*), F_1, F_2 and F_3 were planted in small plastic pots in the green house and then transplanted to the field. All plants were recorded on an individual plant basis. The quantitative characters were evaluated as follows:

Flowering time—recorded as number of days from June 17 (the planting date) to the date when first flower appeared on the plant.

Maturity date—records were taken at 3 day-intervals as to the number of days after June 17 when more than 90% of the pods on a plant had turned black or brown.

Period from flowering to maturity—number of days between flowering time and maturity date.

Plant height—measured to the nearest centimeter when the plant was harvested.

Number of nodes on main stem—counted on every plant when the height notes were taken.

Seed size—measured in grams per 100 seeds.

Many qualitative characters were recorded. But only a few of them showed distinct contrasting characters. These were young stem color (purple or green), flower color (purple or white), pod color (black or light brown), bloom on seed coat (bloom or smooth), and seed coat color (black, yellow or yellowish green).

Randomized block design was used with four replications. Each block contained 52 plots. Of these 52 units, 3 were given to each parent (P_1 and P_2), 3 to F_1, 23 to F_2 and 1 to each of the 20 F_3 lines. In each single row plot, 5 plants were planted with 60 cm. between adjacent plants. Plots were 80 cm. away from each other.

Due to an injury from a typhoon early in the growing, many young plants died before reaching maturity, especially P_1 and P_2 plants, because the P_1 had

no bamboo support and the P_2's tissue was still too soft to resist the storm. Also, virus disease infected a portion of plants. Some of them still persisted to maturity but were quite unhealthy. Because of these factors some adjustments were made in the final analysis of data.

1. Only F_1's data was used for evaluating environmental variation of quantitative characters.

2. Plots which had 2 or more plants infected with mosaic or died before harvest were discarded in the analysis.

3. Usually one plant had mosaic or died in each plot. For the sake of simplication, the records of 4 healthy plants in each plot were picked out randomly for computation.

After these changes, data on 320 F_2 plants (20 plots in each block), 19 F_3 progenies (304 plants, one line omitted) and 48 F_1 plants (3 plots in each block) could be used.

Scaling tests and partition of variance components were made according to Mather's methods (1949). Genotypic correlations were estimated using the method suggested by Burton (1951) and Weber and Moorthy (1952). Several formulae were used to calculate heritability. The number of genes was estimated using three different methods given by Mather (1949).

Results and Discussion

The results will be divided in two main parts, the qualitative and the quantitative inheritances of characters concerned. Five qualitative characters and six quantitative characters will be reported in detail.

A. *Qualitative characters*

Five characters, young stem color, flower color, pod color, bloom on seed coat and seed coat color, have simple genetic behaviors. The F_2 segregation ratios are presented in Table 1. And the genetic behaviors of F_3 progenies of

Table 1. Segregation ratios for five qualitative characters in the F_2 generation.

Characters	Theoretical Segregation Ratio	Number of Plants	Observed & Expected Number	X^2	P	Symbol of Alleles
Young stem color	3:1	392	301(294):91(98)	0.67	0.40–0.50	W-w
Flower color	3:1	392	301(294):91(98)	0.67	0.40–0.50	W-w
Pod color	15:1	392	368(367.5):24(24.5)	0.01	0.90–0.95	L_1-l_1, L_2-l_2
Bloom on seed coat	9:7	392	242(220.5):150(171.5)	4.79	0.02–0.05	B_1B_1, B_2-b_2, B_3-b_3
Seed coat color	9:3:4	392	239(220.5):77(73.5):76(98.0)	6.66	0.02–0.05	R_1R_1, TT G-g, i^f-i

the selected F_2 parents are shown in Table 2. Since there were only 12–20 plants in each of the 20 F_3 families, the analysis within each family was not quite reliable. Theoretical segregation ratio was computed from the segregating families pooled together, and the observed ratio was tested with this hypothetical ratio. These results are preseneted in Table 3.

Table 2. Distribution of F_3 families under each character of the F_2 parents

Characters		No. of selected F_2 parents	Segregating and non-segregating F_3 families		X^2	P
			Theoretical ratio	Observed and expected number		
Young stem color & flower color	Purple	17	2:1	10(11.33):7(5.67)	0.46	0.40–0.50
	White	3	—	all white	—	—
Pod color	Black	15	8:7	8(8.00):7(7.00)	0.00	1.00
	Light brown	5	—	all light brown	—	—
Bloom on seed coat	Bloom	13	8:1	12(10.56):1(1.44)	0.14	0.70–0.80
	Smooth	7	—	all smooth	—	—
Seed coat color	Green	11	8:1	11(9.78):0(1.22)	1.37	0.20–0.30
	Yellow	5	2:1	3(3.33):2(1.67)	0.98	0.30–0.40
	Black	4	—	all black	—	—

Table 3. Segregation ratios for five qualitative characters in pooled segregating F_3 families

Characters	Theoretical ratio in pooled seg. familes	Number of segregating families	Number of plants	Observed & expected number	X^2	P
Young stem color and flower color	3:1	10	198	114(118.5):54(49.5)	0.58	0.40–0.50
Pod color	27:5	8	127	110(107.15):17(19.85)	0.48	0.40–0.50
Bloom on seed coat	21:11	12	194	115(127.34):79(66.66)	3.47	0.05–0.10
Seed coat color	21:11:8	14	203	105(106.57):62(55.83):36(40.60)	1.22	0.50–0.60

According to the above tables, the genetic constitutions of the parents may be as follows:

Taichung Green: ww $l_1l_1l_2l_2$ $B_1B_1b_2b_2b_3b_3$ R_1R_1ttggi^{f}i^f.

G. formosana: WW $L_1L_1L_2L_2$ $B_1B_1B_2B_2B_3B_3$ R_1R_1TTGGii.

Young stem color and flower color seemed to be controlled by one single pair of genes (W-w), because green young stem-white flower or purple young stem-purple flower always appeared together. This result was similar to that of varietal crossings. Pod color which was reported by former investigators to be controlled by one pair of genes, L-1 could hardly be confirmed in this study as we observed it. The expected ratio of plants with black or dark pod to plants with light brown pod in the F_2 generation was 15:1. Apparently it was conditioned by two pairs of duplicate genes. Symbols L_1-l_1 and L_2-l_2 were proposed to designate the duplicate genes. According to Weiss (1949) three complementary genes are required for the occurrence of bloom on seed coat. In this experiment, however, only two of them showed segregation, indicating that both parents seemed to have one locus possessing the dominant gene in homozygous condition. The ratio in the F_2 generation (9:7) was a poor fit. But the hypothesis was further substantiated by the analysis of F_3 data (Table 2 & 3). Seed coat color can be classified into three classes, i. e. green, yellow and black. Weiss (1949), reported that R_1 and T were complementary genes for the expression of black seed coat and hilum, and T also was responsible for tawny pubscence. G-g were a pair of alleles conditioning the green (G) and yellow (g) seed coat. Green and yellow colors could express themselves only when the black pigments were inhibited by some inhibitor gene, e. g. I-complete inhibitor, i^i-partial inhibitor, which would prevent the formation of black pigments in the hilum (Weiss, 1949). Both of the parents used in this experiment had tawny pubscence and black hilum. Therefore, R_1 and T must be homozygous in the F_1 and later progenies. A 9 green: 3 yellow: 4 black ratio in the F_2 generation suggested that parents were different with respect to the loci controlling plastid pigments (G-g) and inhibition (i^i-i). Although the segregation ratio in the F_2 generation was a poor fit, further evidences were derived from the F_3 data. For example, all F_3 progenies of four black colored F_2 parents had black seed coat, which were evidently produced by plants with genotype R_1R_1TTG-ii or $R_1R_1TTggii$. Two F_3 progenies in five yellow colored F_2 parents showed homozygous yellow seed coat. They were the progenies of genotype $R_1R_1TTggi^ii^i$. The remaining three segregating progenies showed a segregation ratio of 3 yellow:1 black (X^2=1.29, P=0.20–0.30), which might come from the genotype $R_1R_1TTggi^ii$.

Interrelations among characters were also studied. The results of independency tests between paired combinations of five qualitative characters in the F_2 generation are listed in Table 4. From this Table, it can be seen that no linkage existed between flower color (or young stem color) and pod color. The same was also true of flower color and bloom on seed coat, flower color and seed coat color, pod color and seed coat color, and pod color and bloom on seed coat. The test between seed coat color and bloom on seed coat indicated that linkage may exist. This was not in accordance with the investigation of

previous workers. The segregation ratios in the F_2 generation of bloom on seed coat and seed coat color had been reported as a poor fit to the theoretical. By inspection of linkage data, it can be shown that the significant result of combination between bloom on seed coat and seed coat color was mainly due to the less occurrence of plants with smooth and black seed coat. This fact could be hardly explained as a linkage relationship between loci controlling bloom on seed coat and seed coat color. Since the F_1 plants which were used to produce the F_2 generation formed a large proportion of abortive seeds, a selected sample was employed instead. This effect might cause the genotype which could produce the smooth-black seed coat to occupy a less proportion than the expected number in the sample. This discussion is still quite paradoxical, more extensive studies will be necessary.

Table 4. Tests of independence between paired combinations of five qualitative characters

Combined characters		Observed number	Expected number	X^2	P
Young stem color or flower color-pod color	purple-black	286	275.63	3.42	0.30–0.50
	purple-light	15	18.37		
	white-black	82	91.87		
	white-light	9	6.13		
Young stem color or flower color-bloom on seed coat	purple-bloom	186	165.37	5.47	0.10–0.20
	purple-smooth	115	128.63		
	white-bloom	56	55.13		
	white-smooth	35	42.87		
Young stem color or flower color-seed coat color	purple-green	188	165.37	10.63	0.05–0.10
	purple-yellow	53	55.13		
	purple-black	60	73.50		
	white-green	51	55.13		
	white-yellow	24	18.37		
	white-black	16	24.50		
Pod color -bloom on seed coat	black-bloom	229	206.72	5.40	0.10–0.20
	black-smooth	139	160.78		
	light-bloom	9	13.78		
	light-smooth	7	10.72		
Pod color-seed coat color	black-green	224	206.72	7.68	0.10–0.20
	black-yellow	74	68.91		
	black-black	70	91.87		
	light-green	15	13.78		
	light-yellow	3	4.59		
	light-black	6	6.13		

Bloom on seed coat-seed coat color	bloom-green	149	124.03		
	bloom-yellow	37	41.34		
	bloom-black	56	55.13	20.04	<0.01
	smooth-green	90	96.47		
	smooth-yellow	40	32.16		
	smooth-black	20	42.87		

B. *Quantitative characters*

1. Means, distributions and the criteria of scaling.

Frequency distributions for six quantitative characters studied are shown in Figures 1, 2, 3, 4, 5 and 6. The ranges and means of P_1, P_2, F_1, F_2 and F_3 generations and the mid-parent values are listed in Table 5. Because of abnormal growth, no parental data were available for seed size. To make comparison, records for seed size of P_1 and P_2 are cited from another paper (Tang *et al* 1959).

Table 5. Ranges, means, mid-parental values of six quantitative characters

	No. of plants	Range	Mean	Standard error
Flowering time		days (date)		
P_1	48	32-39(7.20-7.27)	35.8571	0.2041
P_2	33	90-98(9.16-9.24)	92.3939	0.3939
F_1	48	54-67(8.9-8.24)	59.2500	0.3186
F_2	320	40-76(7.28-9.2)	60.9750	0.4330
F_3	304	39-81(7.27-9.7)	60.0066	0.5172
M			64.1225	0.2218
Maturity date		days (date)		
P_1	48	96-105(9.22-10.1)	102.7755	0.4011
P_2	33	132-143(10.28-11.8)	140.0030	0.4636
F_1	48	102-111(9.28-10.7)	106.8125	0.4040
F_2	320	93-138(9.17-11.3)	107.7437	0.3939
F_3	304	96-138(9.20-11.3)	106.3520	0.3915
M			121.8893	0.3062
Period from flowering to maturity		days		
P_1	48	61-73	68.0638	0.4484
P_2	33	41-52	47.0909	0.5095
F_1	48	40-53	47.5000	0.4456
F_2	320	31-71	46.9063	0.3862
F_3	304	33-64	46.2796	0.3676
M			57.5774	0.3393
Plant height		cm.		
P_1	48	16-49	29.9592	0.8396

P_2	27	210-240	256.0000	9.5443
F_1	48	155-330	259.9375	6.6852
F_2	320	27-340	177.8844	3.7047
F_3	304	13-375	141.7237	3.8218
M			142.9796	4.7489
Number of nodes on main stem				
P_1	48	7-14	10.2979	0.2736
P_2	27	23-55	35.8148	1.6913
F_1	48	23-44	34.6042	0.6404
F_2	320	8-47	27.0906	0.3928
F_3	304	8-41	23.8684	0.4100
M			23.0563	0.8566
Seed size		gm./100 seeds		
P_1	—	—	11.8*	—
P_2	—	—	0.8*	—
F_1	48	1.9-4.2	3.1479	0.0692
F_2	275	0.8-6.5	2.8425	0.0598
F_3	225	1.2-5.9	2.5622	0.0621
M			6.3	

M=mid-parent value

* data cited from Tang *et al.* (1959).

Flowering time appeared to have similar means among the F_1, F_2 and F_3 generations but they were slightly earlier than the mid-parent. Maturity date, period from flowering to maturity and seed size also had nearly equal means among the F_1, F_2 and F_3 generations. But the former character approched its cultivated parent, and the latter two characters obviously shifted toward the wild parent. The F_1-mean values of plant height and number of nodes on main stem approximated those of wild parent and a depression of means in later generations toward their mid-parent values were observed.

Scaling tests were made for six characters using formulae as follows:

$A=4F_2-2F_1-P_1-P_2$

$B=16F_3-4F_2-2F_1-P_1-P_2$.

Both the original scale and the logarithmic scale were tested (except for seed size), but both were found to be inadequate for the analysis of variation. Several reasons are proposed for the ineffectiveness of the criteria of scaling in the experiment.

1. The plants, whose seeds were used for propagating the F_2 and F_3 generations in the experiment, formed many empty pods and abortive seeds. If this phenomenon had something to do with the genotype of the young zygote, then it might not fall in with the assumptions upon which scaling test were made.

2. As seeds were sown in the plastic pots and then transplanted to the field after one week, the workers had a tendency to choose the more vigorous seedlings for transplanting. Such a practise might affect the genotypic constitution of the later generations.

3. The abnormal growth of the P_1 and P_2 plants made the records taken for the various characters quite unreliable. Furthermore, many plants in the F_2 and F_3 generations died before maturity, especially those which resembled the parents in growth habit. In this way, selection seemed to be in favor of plants that were more or less like the F_1 in appearance and therefore they tended to occupy a larger proportion in the later generations.

4. Perhaps there were strong effects of interallelic interactions or environment-genotype interaction, which made the scales inadequate.

Perhaps the last departure would account more for the inadequacy of the scales used. Somehow, all causes might operate simultaneously. Since neither of the scales used (i. e. original scale or logarithm) could be regarded as satisfactory, only the original scale was used for the sake of simplification in analysis.

2. Components of variance.

The partitioning of variance were carried out in accordance with Mather's methods (Mataer, 1949). Two sets of equations were used:

$$\left.\begin{array}{l} V_{F_2} = \frac{1}{2}D + \frac{1}{4}H + E_1 \\ V_{\bar{F}_3} = \frac{1}{2}D + \frac{1}{16}H + E_2 \\ \overline{V}_{F_3} = \frac{1}{2}D + \frac{1}{8}H + E_1 \\ \left.\begin{array}{l} E_1 \\ E_2 \end{array}\right\} \text{direct estimates} \end{array}\right\} \text{(for five characters other than seed size)}$$

$$\left.\begin{array}{l} V_{F_2} = \frac{1}{2}D + \frac{1}{2}H + E_3 \\ V_{F_3} = \frac{3}{4}D + \frac{3}{16}H + E_3 \\ W_{F_2/F_3} = \frac{1}{2}D + \frac{1}{8}H \\ E_3: \text{ direct estimate} \end{array}\right\} \text{(for seed size)}$$

where

D = fixable genetic component

H = non-fixable genetic component

E_1 = non-heritable component within plots

E_2 = non-heritable component between plots

E_3 = gross environmental effects, non-heritable

The results are presented in Table 6.

Table 6. D (fixable genetic variance), H (unfixable genetic variance). E_1, E_2 and E_3 (environmental variance) values for six quantitative characters

Components	Estimate	Standard error
	Flowering time (No. of days)	
D	128.8070**	19.2818
H	-21.6663	52.9090
E_1	1.4468	4.5280
E_2	1.1047	4.9602
	Maturity date (No. of days)	
D	50.7802**	3.9258
H	71.3134**	10.7725
E_1	2.8776*	0.9219
E_2	0.4046	1.0099
	Period from flowering to maturity (No. of days)	
D	24.2131**	1.5599
H	95.3794**	4.2802
E_1	8.7258**	0.3663
E_2	1.4365*	0.4013
	Plant height (cm.)	
D	4,107.5740	1,923.0285
H	2,432.7904	5,276.7465
E_1	1,463.9190*	451.5926
E_2	156.5280	494.6949
	Number of nodes on main stem	
D	35.7018**	1.4997
H	69.7305**	4.1151
E_1	16.5272**	0.3521
E_2	3.0931**	0.3857
	Seed size (gm./100 seeds)	
D	0.1603*	0.0533
H	2.6648**	0.1763
E_2	0.2383**	0.0156

* Significant at the 5% level
** Significant at the 1% level

Variation in flowering time, maturity date, period from flowering to maturity, number of nodes on main stem and seed size seemed to be caused by additive genetic effects, while that of maturity date, period from flowering to maturity, number of nodes on main stem and seed size was caused to a large extent by dominance. Excepting flowering time, the other five quantitative characters were influenced more or less by environmental factors.

3. Phenotypic and genotypic correlations.

Genotypic correlation coefficients were estimated using formula proposed by Burton (1951) and Weber and Moorthy (1952). The variances and covariance of F_1 were calculated and subtracted from the total variances and covariance of F_2 (or F_3), respectively. Then the derived genotypic variances and covariance were used to calculate the genotypic correlation coefficients for six quantitative characters in the F_2 (or F_3) generation. The calculation method of phenotypic correlation corfficients is the same as above. The environmental correlation coefficients in the F_1, phenotypic and genotypic correlation coefficients for six quantitative characters in the F_2 and F_3 generations are presented in Table 7.

Table 7. Phenotypic and genotypic correlation coefficients between quantitative characters in the F_2 and F_3 generations

Characters correlated	Phenotypic correlation coeff.			Genotypic correlation coeff.	
	F_1 popu'n	F_2 popu'n	F_3 popu'n	F_2 popu'n	F_3 popu'n
Flowering time and					
maturity	0.2867*	0.5565**	0.7399**	0.6433	0.8401
period from f. to m.	-0.4839**	-0.7919**	-0.5759**	-0.8539	-0.6108
plant height (cm.)	-0.0583	0.1698**	0.3961**	0.2732	0.6318
No. of nodes	0.1033	0.0598	0.3870**	0.0530	0.5176
seed size (gm./100 seeds)	-0.2991*	-0.4794**	-0.5024**	0.5221	-0.5515
Maturity date and					
period from f. to m.	0.6684**	0.1399*	-0.1039	-0.0400	-0.3631
plant height (cm.)	0.4342**	0.1656**	0.3243**	0.0688	0.2809
No. of nodes	0.3883**	0.1131	0.3190**	0.0224	0.2941
seed size (gm/100 seeds)	0.1289	-0.2535**	-0.1921**	-0.3974	-0.2910
Period from flowering to maturity and plant height (cm.)	0.4234**	-0.1214*	-0.1720*	-0.3963	-0.5606
No. of nodes	0.2231	-0.0118	-0.1203	-0.1076	-0.3042
seed size (gm/100 seeds)	0.4076**	0.2716**	0.4164**	0.2248	0.4191
Plant height (cm.) and					
No. of nodes	0.4956**	0.6763**	0.7655**	0.8247	1.0491
seed size (gm/100 seeds)	0.2649**	-0.1236*	-0.1494*	-0.3495	-0.2599
Number of nodes on main stem and seed size (gm/100 seeds)	0.1052	-0.1351*	-0.1449*	-0.2852	-0.2748

* Significant at the 5% level
** Significant at the 1% level

In general, correlations between characters in the F_3 generation were higher than those in the F_2 generation and genotypic correlations were higher than

the phenotypic correlations, so that all the genotypic correlation coefficients in the F_3 generation, both positive or negative, were rather large in magnitude. The positive correlations between flowering time and maturity date, plant height and number of nodes on main stem and the negative correlation between flowering time and period from flowering to maturity were consistently high for either phenotypic or genotypic measurements in the segregating generations.

4. Heritability.

Heritability of characters was estimated by the following formulae:

a. $\frac{V_{F_2}-V_{F_1}}{V_{F_2}}$, where V_{F_1}=observed E_1 for five quantitative characters excepting seed size, or E_3 for seed size.

b. $\frac{W_{F_2/F_3}}{V_{F_2}}$, this formula was only used for seed size.

c. $\frac{V_{\bar{F}_3}-V_{\bar{F}_1}}{V_{\bar{F}_3}}$, where $V_{\bar{F}_1}$=observed E_1. Heritability of seed size can not be estimated by this formula.

d. $\frac{\frac{1}{2}D}{\frac{1}{2}D+\frac{1}{4}H+E_1}$ and

e. $\frac{\frac{1}{2}D}{\frac{1}{2}D+\frac{1}{16}H+E_2}$, where D, H, E_1 and E_2 are expected values cited from Table 6. For the estimation of the heritability of seed size, E_1 or E_2 in the last two formulae was replaced with E_3. Formulae a, b and c were used to estimate the heritability of a character in the broad sense while d and e were used to measure it in narrow sense. Theoretically, if non-fixative genetic or dominant effect is prominent, the values of heritability will be variable, otherwise all estimates will give similar results. The values of heritability estimated from the above five methods are shown in Table 8.

Table 8. Heritability estimates for six quantitative characters by different formulae

Estimate formulae	Flowering* time	Maturity date	Period from flo. to mat.	Plant height	No. of nodes	Seed** size
a	91.88	84.22	80.03	51.16	60.30	76.64
b	—	—	—	—	—	41.32
c	98.28	98.40	92.91	91.42	70.55	—
d	97.80	55.08	28.85	49.78	24.45	8.13
e	98.31	83.93	64.77	86.94	87.77	16.52

* The negative H value of flowering time replaced with 0.

** The E_1 and E_2 components replaced with E_3 in the computation of seed size.

In general, we can see that heritability values or the five characters excepting flowering time were considerably low when calculations were made by formula d. Excluding seed size, higher values were obtained by the other formulae.

5. Number of effective factors and gene action.

Three formulae were used according to Mather's methods:

a. $K_{1a} = \frac{(\overline{P}_1 - \overline{P}_2)^2}{2}/D$

b. $K_{1b} = (\overline{F}_1 - M)^2/H$

c. $K_2 = {}_H\overline{V}_{F_3}/({}_HVv_{F_3} - \frac{2}{n-1}\overline{V}_{F_3})$

where $\overline{P}_1$, $\overline{P}_2$ and $\overline{F}_1$ are means of parents and F_1 hybrid, M is the midparent value, $\overline{V}_{F_3}$ and Vv_{F_3} are the mean variance of the F_3 progenies and variance of the F_3 variances respectively. The sub-H in front of V indicates that it is the heritable portion of variance. As an estimate of the number of effective factors, K_2 is superior to K_{1a} or K_{1b} is not being subject to reduction by incomplete concentration or reinforcement of allelomorphs. But if K_{1a} or K_{1b} is not reduced in value from lack of full concentration or reinforcement, they are superior to K_2. However, unequal estimates among K_{1a}, K_{1b} and K_2 will lead to underestimation of the number of factors. But these values can be used to judge the gene action, i. e. variation in the effects of individual factors (the d increments) and dominant units (the h increments). The number of factors estimated by these formulae for six characters are presented in Table 9.

Table 9. Estimates of the number of effective factors conditioning the expression of six quantitative characters by different formulae

Characters	K_{1a}	K_{1b}	K_2
Flowering time	6.20	—	1.90
Maturity date	7.19	3.18	1.19
Period from flo. to mat.	4.54	1.06	2.01
Plant height	12.44	5.62	0.38
No. of nodes	4.56	1.91	1.96
Seed size	—	3.84	0.94

The unequal values among K_{1a}, K_{1b} and K_2 indicate that the effects of individual factors and dominant units were highly variable. Since parents used in this experiment were extremely different for characters concerned, isodirectional distribution of genes controlling quantitative characters might exist in parents. This would suggest that K_{1a} might be more accurate than K_{1b} or K_2.

Summary and Conclusions

Five qualitative characters showed simple genetic behaviors. Except pod-color, which was found to be controlled by two duplicated alleles in this study, the other four characters, young stem color, flower color, bloom on seed coat and seed coat color, gave similar results as reported by other investigations. No evidence of linkage relationships was detected. The significant result of independency test between bloom on seed coat and seed coat color was in fact due to another cause.

Scaling test showed that neither the original scale nor the logarithm was adequate. Several reasons were proposed for the explanation thereof. Six quantitative characters, flowering time, maturity date, period from flowering to maturity, plant height, number of nodes on main stem and seed size were analyzed on the original scale.

Significant additive genetic effects existed in the variances of flowering time, maturity date, period from flowering to maturity, number of nodes and seed size. Dominant effects were rather great in the variances of maturity date, period from flowering to maturity, number of nodes and seed size. Environmental factors influenced five characters other than flowering time to a certain degree.

Correlations between quantitative characters were computed. The results agreed with those of other investigators (Weber, 1950; Johnson *et al*, 1955). In general, genotypic correlation coefficients were higher than phenotypic correlation coefficients and closer correlations between characters in the F_3 generation were observed.

On the average, five out of the six characters had considerably high heritability value. The heritability values were very low when genetic variance ($\frac{1}{2}D$) was used as heritable portion.

Unequal estimates of the number of effective factors by means of three different formulae indicated that the effects of individual factors and dominant units (i. e. the d and h increments) were highly variable. However, K_1^a might offer more accurate estimates.

Acknowledgment

The authors wish to express their heart-felt thanks to Dr. Chung-fu Cheng for his encouragements and to J. C. R. R. for the financial aid.

大豆種間雜種 (*Glycine max* × *G. formosana*) 後代遺傳行為之研究

湯 文 通 戴 喬 治

1. 本研究開始於 1958 年，研究內容分兩部分，一爲質的性狀之遺傳，另一爲量的性狀之遺傳。

2. 五個質的性狀可確定其遺傳模式，幼莖色與花色共受一對因子之控制 (W—w)；莢色爲二對重複因子 (L_1—l_1, 及 L_2—l_2) 控制；種皮粉衣爲三對互補因子之遺傳，但本研究兩親本間僅有兩對因子互異 (B_2—b_2 及 B_3—b_3)，種皮色澤之 F_2 分離比則爲 9 黃綠色：3 黃色：4 黑色，其雙親因子型各爲 R_1R_1TTGGii (*G. formosana*) 與 R_1R_1TTggi^{i}i^i (臺中青皮豆)。

3. 除種皮粉衣與種皮色澤兩性狀間外，其他性狀間均無連繫關係之存在。惟種皮粉衣與種皮色澤間的密切關係，似亦因其他原因造成，而與連繫無關。此尚待繼續追究。

4. 六個量的性狀：開花期，成熟日數，開花—成熟日數，株高，主莖節數及種子大小 (百粒重)，其遺傳行爲均作詳細探討，結果如次。

5. 開花期，成熟期，開花—成熟日數，主莖節數及種子大小諸性狀有顯著累加遺傳效果。顯性效果則在成熟期，開花—成熟日數，主莖節數及種子大小諸性狀變方中佔重要地位。除開花期外，其他性狀均顯然受環境之影響。

6. 一般言之，因子型相關大於外表型相關。開花期與成熟期，株高與主莖節數有最大正相關，而開花期與開花—成熟日數有最大負相關。

7. 開花期有最高遺傳力，除種子大小外，其他諸性狀以 F_3 系平均變方計算遺傳力時，其值均相當高。

8. 諸性狀之控制因子的個別效果及各顯性單位的效果均具甚大變異性，因此有效因子數之估計均過低。大略言之，應在下列各數以上，開花期：6，成熟期：7，開花—成熟日數：5，株高：12，主莖節數：5，種子大小：4。

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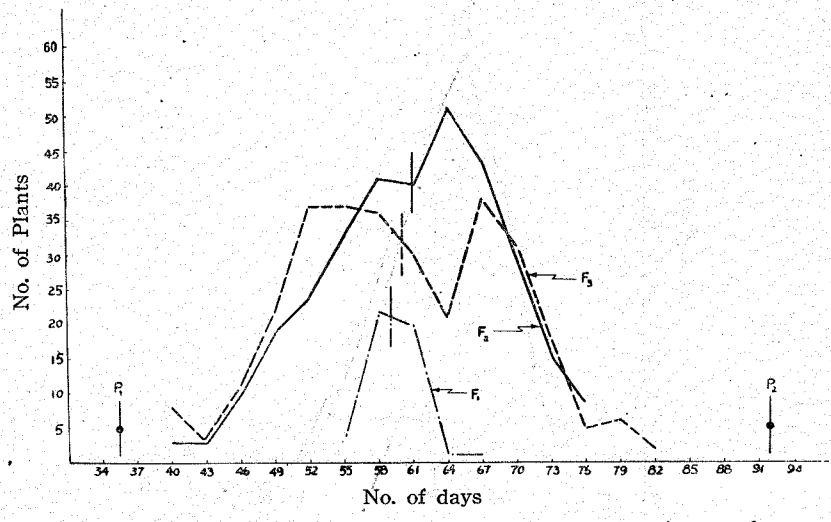

Fig. 1. Frequency distributions of the F_1, F_2 and F_3 generations and mean values of parents for flowering time.

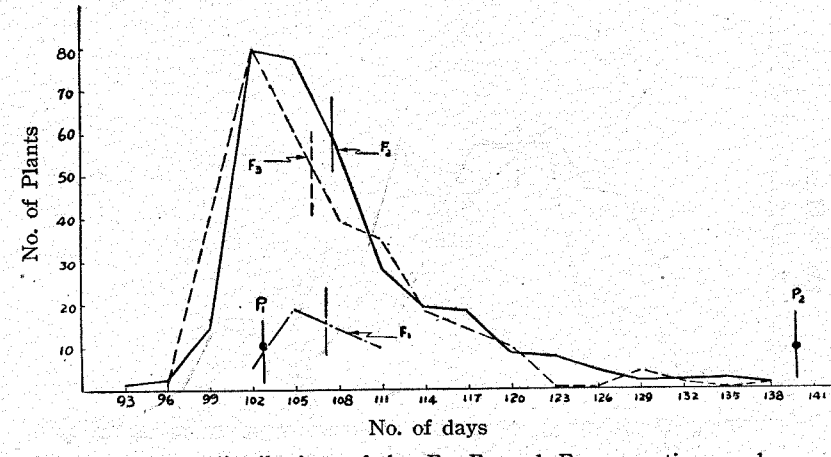

Fig. 2. Frequency distributions of the F_1, F_2 and F_3 generations and mean values of parents for maturity date.

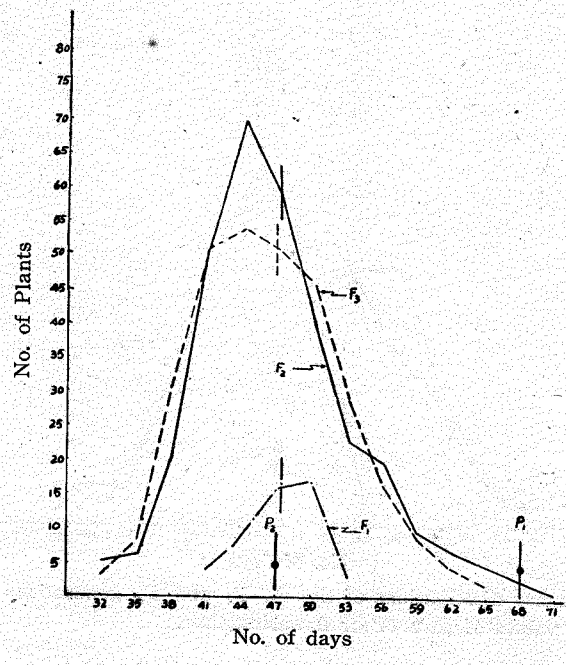

Fig. 3. Frequency distributions of the F_1, F_2 and F_3 generations and mean values of parents for period from flowering to maturity.

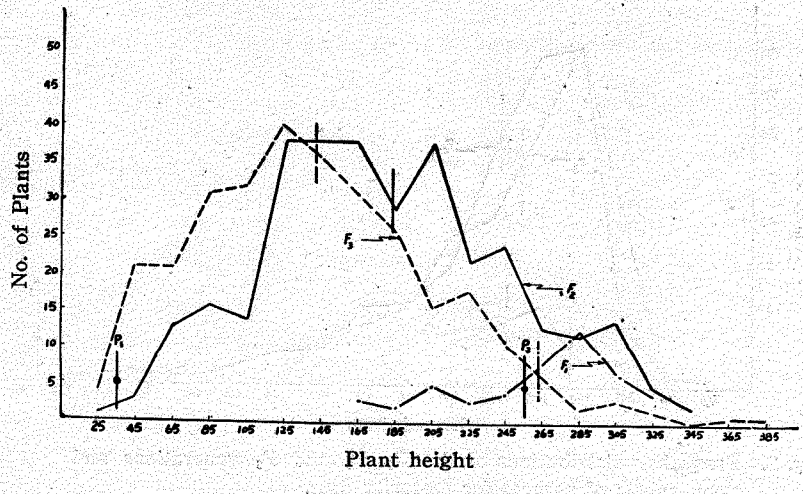

Fig. 4. Frequency distributions of the F_1 F_2 and F_3 generations and mean values of parents for plant height (cm).

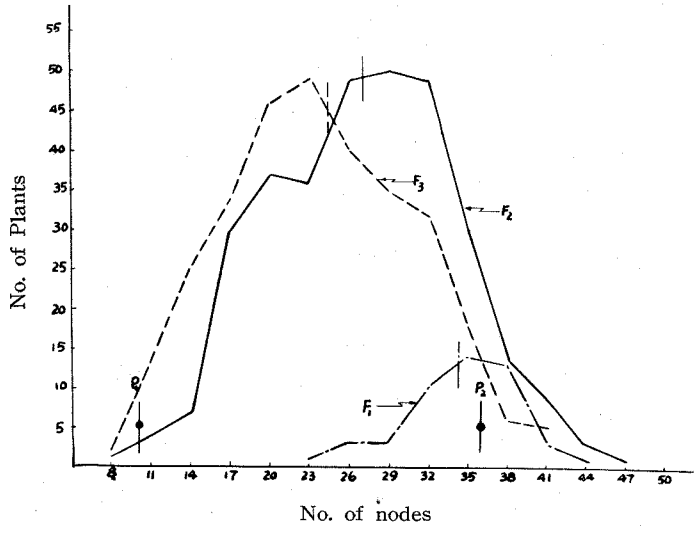

Fig. 5. Frequency distributions of the F_1, F_2 and F_3 generations and mean values of parents for number of nodes on main stem.

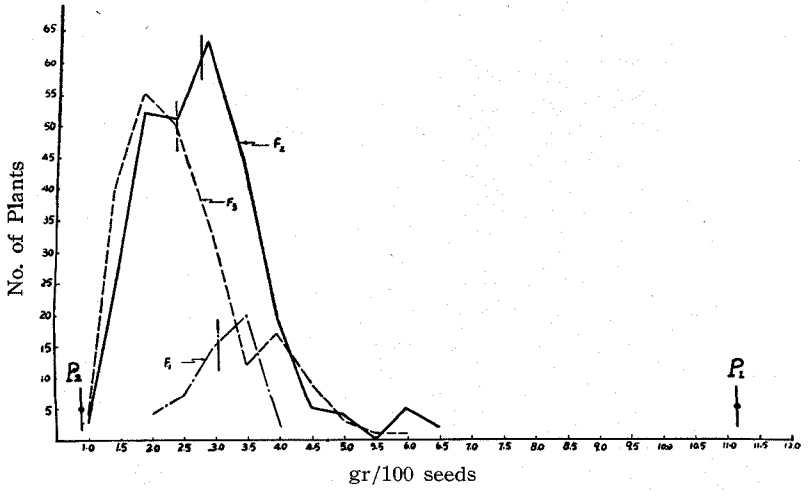

Fig. 6. Frequency distributions of the F_1, F_2 and F_3 generaions and mean values of parents for seed size (gm./100 seeds).

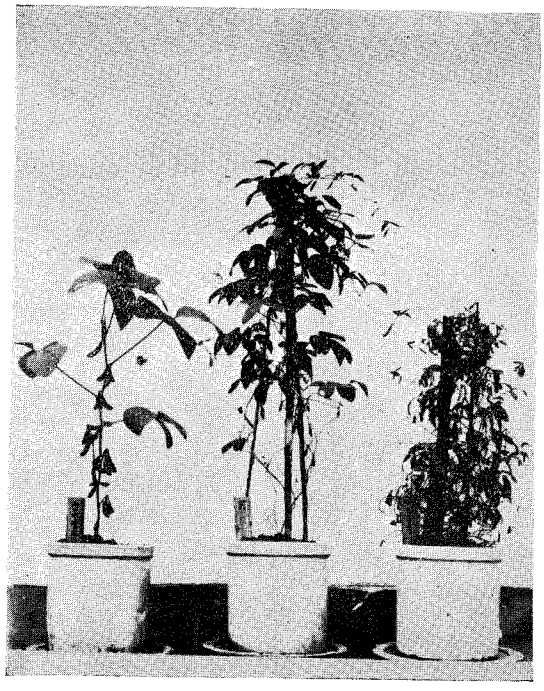

Fig. 7. Left: Taichung Green. Middle: F_1. Right: *G. formosana.* (in the green house)

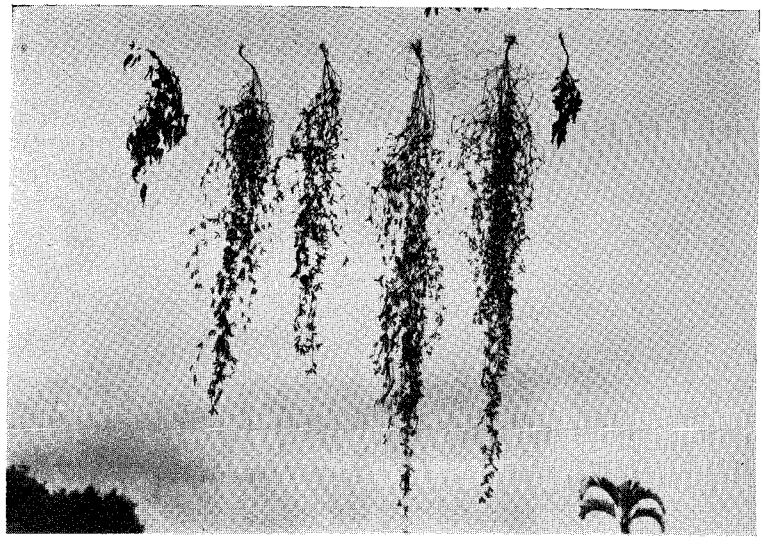

Fig. 8. Taichung Green (1st plant from right), F_1 (2nd plant from right) and different types of F_2 plants.

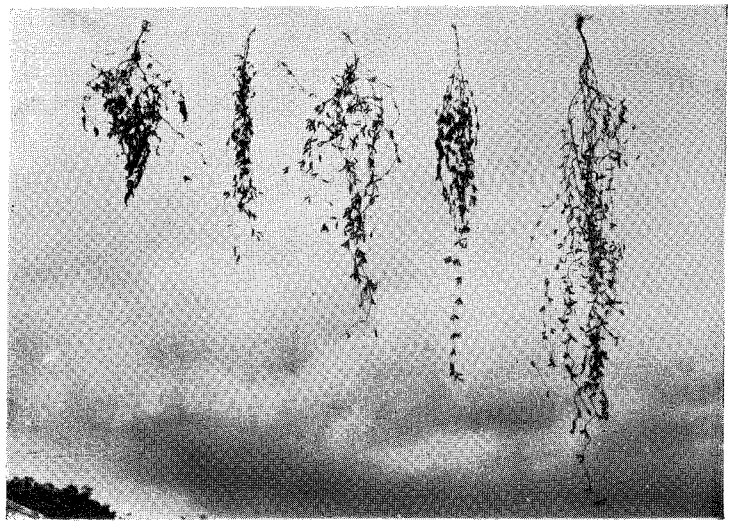

Fig. 9. Different types of F_3 plants.

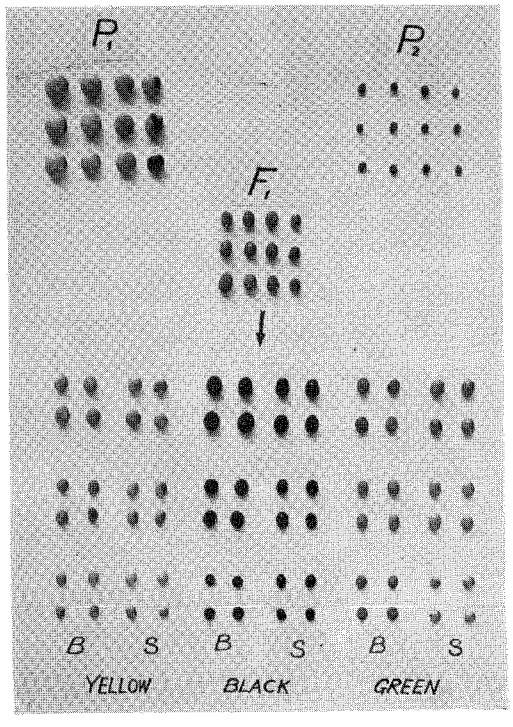

Fig. 10. Segregation of seed size, seed coat color and bloom on seed coat. B; bloom. S; smooth.

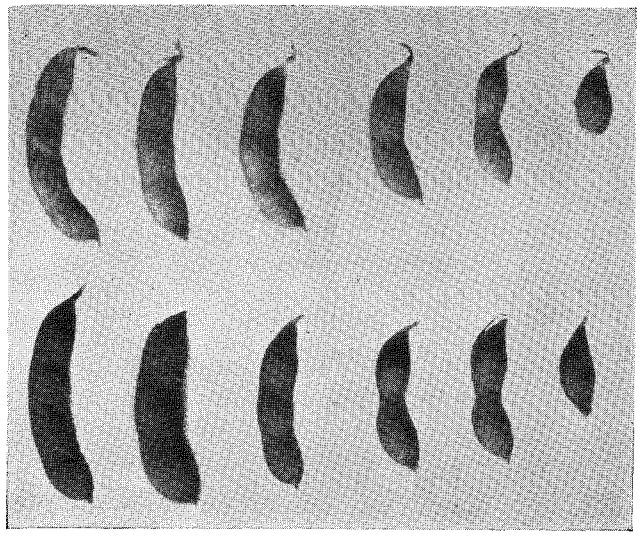

Fig. 11. Black (below) and light (above) colored pods.